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STUDIES OF THE DESERT TORTOISE, *GOPHERUS AGASSIZII*

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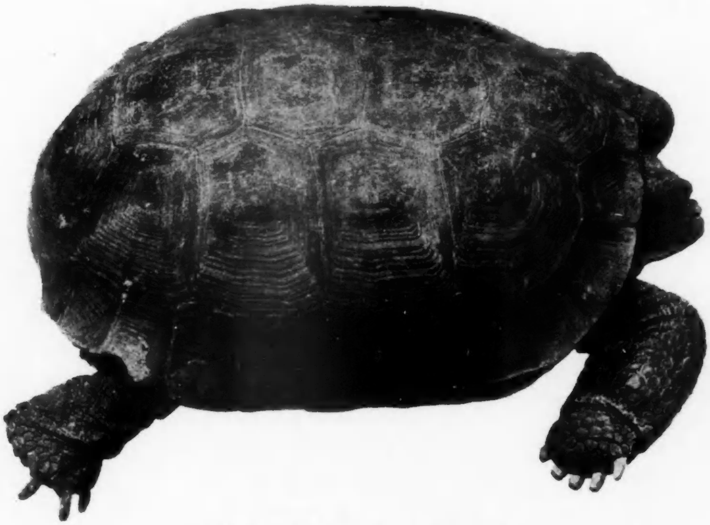

The Desert Tortoise, *Gopherus agassizii*

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STUDIES OF THE DESERT TORTOISE, *GOPHERUS AGASSIZII*

INTRODUCTION

A stable colony of the desert tortoise, *Gopherus agassizii,* that lives on the Beaver Dam Slope in extreme southwestern Utah, where the temperature extremes of the desert environment transcend the lethal limits of cold-blooded vertebrates provided material for the studies upon which this report is based. This is the first of a series of papers planned to deal with reptiles and their adaptations that are shown chiefly by their behavior patterns in the arid regions of interior western North America.

Three trips into the area between April, 1930 and August, 1935 introduced the authors to some of the summer activities of tortoises. Additional work was initiated on November 28, 1936 when, after two days of searching, the discovery of the first hibernation dens gave clues to the tortoise winter behavior.

On this day, twelve tortoises congregating in a horizontal tunnel in the gravelly bank of a wash, which was later named Big Den (Fig. 25), were provided with recognition marks by placing red paint on different scutes of the carapace. This was the first of about 90 trips each of one to four days duration within the following 10-year period, during which 281 tortoises were individually marked and 812 recaptures were recorded, making a total of 1093 tortoise records from the area.

Acknowledgment of assistance and services from various staff members of the University of Utah and the Dixie Junior College is made with thanks and appreciation. Numerous students have assisted in the project, among whom especial mention should be made of the following: O. S. Walsh, Max A. Woodbury, LaMont C. Cole, John Vasquez, Dixon M. Woodbury, J. Walter Woodbury, and Henry W. Setzer from the University of Utah; Harold G. Higgins, Orlo Hall, Vere Barnhurst, Grant Pope, Rex Bleak, Alpine Shirts, and Alpine Prince of the Dixie Junior College. Thanks are also given to Professor Charles D. Winning of New York University for assistance; to Mr. Harold J. Burback of the U. S. Grazing Service, Salt Lake City and to Mr. Wilfrid M. Hasfurther of U. S. Soil Conservation Service at St. George for the use of aerial maps of the region; to the California Academy of Science for use of certain engravings; to Dr. Lowell A. Woodbury for assistance in the treatment of statistics; and to Dr. R. V. Chamberlin and L. M. Klauber for advice regarding the manuscript.

REVIEW OF THE LITERATURE

The desert tortoise was first described as *Xerobates agassizii* by Cooper (1863:120) from a specimen taken near Fort Mohave, California. It was treated under this genus by Cooper (1870:67) and by True (1882:437 and 1883:38). It was referred by Boulenger (1889:156) in his catalog of chelonians in the British Museum to the enormous genus Testudo. He has been followed in this allocation by Ditmars (1907:69), Siebenrock (1909:517), Camp (1916:512), Grinnel & Camp (1917:199), Cowles (1920:64), Terron (1921:165), and Miller (1932:189).

It was transferred to the genus Gopherus by Stejneger (1893:161), to which it has been consistently referred in all editions of the Stejneger & Barbour Check-list of North American Amphibians and Reptiles. This allocation has been followed generally by the majority of other writers beginning with Van Denburgh in 1897. Although admitted that Gopherus is difficult to distinguish from Testudo, the present authors regard it as advisable to keep it separate.

Cox (1881:1003) gave interesting natural history notes of this tortoise in southern Arizona. True (1882:437) summarized the literature and gave analyses of characters by means of which the three species could be separated. Stejneger (1893:161) revealed a known extension of its range in his report of the reptiles of the Death Valley expedition.

O. P. Hay's masterly treatise (1908) of the fossil turtles of North America must be cited in this work even though it does not deal with this tortoise. It does, however, give the fossil background and historical perspective into which an understanding of the skeletal relationships of this species must fit and from which much of the skeletal nomenclature has been derived.

Camp (1916:512) discussed the distribution of the desert tortoise in southern California and commented on other aspects. He reported burrows north of Goff's railroad station, from 2 to 8 feet long, under bushes and in banks of small dry washes. Hallinan (1923:11-20) described the burrows and some of the egg-laying habits of the Gopher Tortoise, *Gopherus polyphemus,* northern Florida. In 1927, the Ortenburgers (1927:101) published additional natural history notes of the tortoise in southern Arizona.

Van Denburgh & Slevin (1913:397) reported several specimens from Arizona and Van Denburgh (1922:986) gave a careful description, records of its known distribution and a discussion of its habits that contained quotations from Cox (1881:1003), Meek (1905:3), Camp (1916:512) and Stephens (letter).

Vernon Bailey (1928:372) called attention to the remarkable adaptations this tortoise possessed for desert life—its protective shell; its ability to withdraw head, legs and tail into the shell; its ability to go long periods without drinking; but could not find any water storage sacs except the bladder.

In the same year, Tanner (1928:54) included it in his check list of Utah reptiles. Woodbury (1931:121)

discussed it as a member of the Utah reptilian fauna while MacCoy (1932:11) gave further notes on this tortoise in southern Arizona.

The most complete treatment is that given by Loye Miller (1932:187-208). He described the eggs, the hatchling young, the problem of growth rings in the shell, sparse distribution of the adults, food and water, methods of defense, growth rate, diseases, enemies and adaptations.

Grant (1936:225-229) discussed asymmetry, dimorphism, habits, water storage, young, range and statistics of size. The range he described extended from southeastern California, eastward across southern Nevada to Washington County, Utah and southward through Arizona to Sonora, Mexico.

Bogert (1937:191) reported measurements of 3 marked tortoises recaptured near the point of liberation after 680 days, 818 days and nearly 4 years, respectively.

The idea that reptiles have a seasonal pattern of occurrence in the United States was treated by Conant (1938:137) in his study of snakes and turtles in Lucas County, Ohio. He reviewed the work of C. S. Brimley (1925) in North Carolina, L. M. Klauber (1924, 1926, 1931) in California and Arthur Loveridge (1927) in Massachusetts, all dealing with seasonal incidence of snakes.

Pope (1939:237) gave a general summary of the knowledge of this tortoise gleaned from the literature under headings of identification, size, young, the sexes, egg, growth, distribution, habitat, habits, hibernation and estivation, reproduction, mating, food, drinking, defense, captivity and economic value.

Conant (1945:41) described egg-laying and development of young in the Box Turtle—useful for comparison. Goin & Goff (1941:66) reported studies of the rate of growth in the gopher tortoise.

Cagle's study (1944:1-34) of home range, homing behavior and migration in turtles furnished excellent background material for comparison with these studies of the desert tortoise. In dealing with dynamics of aquatic turtle populations, he states: "A group of turtles may occupy a particular section of a lake or stream. . . . Each individual may occupy a home area which may include parts or all of adjacent water bodies, and within which it usually remains until affected by the breeding stimulus, necessity of movement to areas of hibernation, or aberrant habitat changes."

In current literature, many articles, some of which are cited in the bibliography, describe habits and behavior patterns in other species which elucidate general or comparative patterns useful in studying this species. Recently, in discussing the occurrence of this tortoise in Sonora, Mexico, Bogert & Oliver (1945:398) made some comparisons with ***polyphemus*** and ***berlandieri***.

THE AREA OF STUDY

Location

The area studied is on the Beaver Dam Slope west of the Beaver Dam Mountains in Washington County in extreme southwestern Utah (Fig. 25). It is about seven miles east of the Beaver Dam Wash and from ½ to 3 miles north of the Arizona state line. It is in the southwestern part of Township 43 S., R. 18 W., Utah, along the line of the old Mormon Highway of 1870-1875. It is in the lower edge of the foothills in an area cut by several deep washes with gravelly banks. Part of it is located at the mouth of a large dry canyon on an alluvial fan which has about an 8% slope to the southwest and varies in altitude from 3200 to 3500 feet above sea level. The area includes that reported as Station 9 by Hardy (1945:75).

Physiography

The area lies at the eastern edge of the Great Basin Physiographic Province of Atwood (1940:12) where the Carboniferous limestone is exposed on the west side of the Beaver Dam Mountains. The corner of Utah where it adjoins that of Arizona lying on the Nevada state line is located in a sandy desert about two miles west of the Beaver Dam Wash. This wash arises in the Bull Valley Mountains about 20 or 30 miles to the north.

Eastward from the Beaver Dam Wash, a gentle slope much broken with foothills and washes, leads upward to the Beaver Dam Mountains which traverse a course nearly north and south approximately parallel to the wash and about ten miles distant. Southward, from the Utah state line, about six miles in Arizona, the Virgin River cuts through this range in a winding box canyon about 2,000 feet in depth.

The Beaver Dam Mountains form an abrupt barrier that stands athwart the lowland route that extends up the Virgin River from the low deserts of southern Nevada and southern California and cuts off the Dixie Valley above from the Virgin Valley below. The effectiveness of this barrier is not lessened by the box canyon through the mountains since it does not provide a natural passageway along the banks of the river (Hardy 1945:103).

These mountains appear to have marked the ex-

FIG. 1. View of Beaver Dam Slope and Mountains showing Joshua Tree and typical desert shrubs.

treme northeastern limits of the range of the Desert Tortoise until, through the agency of man, the barriers were passed and tortoises were distributed far and wide beyond the mountains. Whether successful colonization of new areas will result from this wide dissemination is not known and probably, because of the long life span and slow rate of reproduction, cannot certainly be determined for many years.

PROCEDURES, METHODS, AND RECORDS

This study is an outgrowth of investigations made on snake dens and was undertaken to provide comparative material for the interpretation of snake behavior in concentrating in winter dens. The first investigations in this area for this purpose were undertaken on November 27 and 28, 1936.

EXPLORATION

Previous summer investigations in 1930, 1932 and 1935 had yielded some preliminary general ideas of summer behavior in which the tortoises had been discovered inhabiting small individual holes well distributed over the desert flats. Careful searching over the same areas on November 27, 1936 failed to reveal a single tortoise. The banks of washes were then searched for holes in which the tortoises might winter. This was done by driving up and down the desert washes southwest of Castle Cliff Service Station on U. S. Highway 91. In the bank of one of the washes, 3 holes were discovered, from which one, two and five tortoises were extracted, respectively.

After fruitless searching in smoother terrain, several dens were found east of the highway in a rougher area with deeper washes and steeper banks along the foot of the mountain (Fig. 25). The largest one found, Big Den, had an opening about 16 inches in diameter of half-moon shape, inside which tortoises could be discerned.

FIG. 2. View of 12 tortoises at the mouth of Big Den at time of original visit on November 28, 1936.

The tortoises near the entrance were removed with the aid of a heavy wire hooked on the distal end. In order to reach the more distant tortoises, a shovel was used to enlarge the opening so that a person could crawl into the tunnel. Thirteen tortoises were removed from the den (Fig. 2). In the deeper part, beyond a curved passageway, there may have been other tortoises that could not be seen. After marking the tortoises, they were replaced in the den and the entrance refilled to natural size.

MARKING TORTOISES

Twelve of the tortoises first taken from Big Den were marked with red paint for individual identification, different scutes being covered in different tortoises. Two years later when additional tortoises were found in nearby dens, they were also painted in a similar manner, but in addition to the individual markings, various colors were applied to indicate the dens in which they were found.

The records show that red paint was applied for den identification to 12 tortoises on November 28, 1936, and to 8 on November, 1937; blue paint to 6, yellow paint to 9, green paint to 5 and red paint to 5 tortoises on November 5, 1938; cream paint to 7 and orange to one tortoise on February 18, 1939.

Soon it became obvious that the paint would wear off and branding was substituted for individual identification, but despite the wearing effect, paint on some of the tortoises remained for several years even though that on others was lost. Of the 9 painted yellow, 5 still contained definite traces of the paint after lapses of 1778, 2261, 2632, and 2640 days, respectively. There is only one record of blue paint after a lapse of 1778 days. There are two records of green after 2647 and 2654 days. The orange paint still showed on the one tortoise after a lapse of 1828 days. There are no records of recaptured tortoises with cream paint.

Of the 25 tortoises marked with red paint, 8 had vestiges of the paint still remaining after lapses of 2261, 2856, 2935, 2977, 2985, 2999, 3354 and 3361 days. While most of the tortoises were branded and hence identifiable without the paint, tortoise F8♂ which was painted at Little Den, November 25, 1937 was not seen again and was thought to be lost until found when Black Top Den was discovered on February 10, 1946 and was definitely identified as the long-lost tortoise by means of the paint.

After the first years, it was noted that the paint marks were beginning to wear and although still plain, it became obvious that they would eventually become unrecognizable. In response to the need for a better method of marking, it was decided to try branding the shells with a hot iron. A small branding iron containing the letter U was prepared by John Vasquez, one of the students, and thereafter all tortoises were branded for individual identification.

At first, the letter U was burned on a different scute on each tortoise until all of the available carapace plates had been utilized. Thereafter, different combinations of two or even three scutes were used. The branding iron was later abandoned in favor of a light curved wire which could be quickly heated over an open fire.

This method proved far superior to painting and was used throughout the study, but it too was beset with inherent problems. If burned lightly on the shell, it would wear off in a few years, whereas if burned too deeply, it would initiate a series of regenerative changes which would ultimately replace the burned portion with a new piece. See "Bone and Its Regeneration."

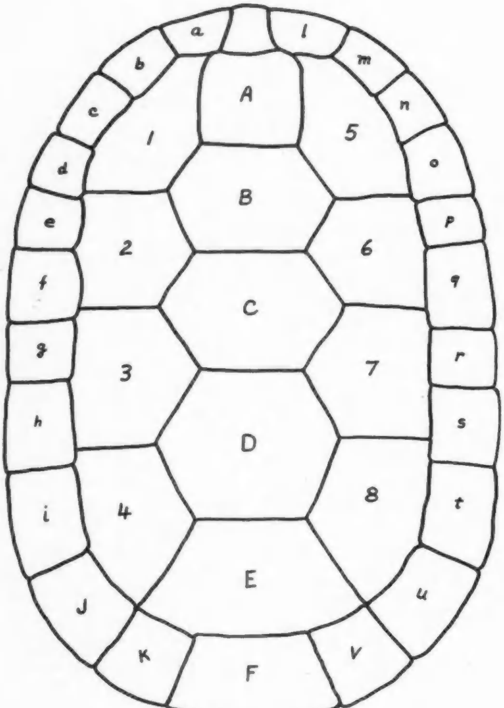


FIG. 3. Sketch of carapace showing arrangement and designation of scutes.

Identification of Tortoises and Dens

When tortoises were recaptured, it became desirable to have some convenient method of identification for record. At first, tortoises were assigned numbers accompanied by a designation of the scutes on which the paint or brand was placed.

This method was later displaced (July, 1939) by a much simpler method. Each dorsal scute was lettered as shown in Figure 3. The vertebrals were indicated by capital letters A to E and the pygal by F. The costals were numbered from 1 to 4 on the left side and 5 to 8 on the right side. The marginals were indicated by small letters from a to k on the left and l to v on the right side.

Identification was then made by citing the proper letters or numbers which referred to the scutes upon which the brands had been placed. This combination with the sex sign following it was used to indicate the individual tortoise, thus B♂, 2d♂, Bfq♀.

When tortoises were recaptured, it also became desirable to have some convenient method of indicating the place of recapture. Names were given to the dens and a map was made showing the location of the winter dens and some of the summer holes. Mimeographed copies of this map were used to record the location of recapture. As the area of study was enlarged and more dens were discovered it became necessary to make a more permanent record of the names of the dens. A wooden peg bearing the name was set in the ground within the entrance of each den (Fig. 17).

Recaptures

Of the 281 tortoises marked, 182 were recaptured a total of 812 times between November 28, 1936 and February 3, 1946. The number of recaptures per tortoise ranged from 1 to 22 with an average of nearly 4.5. The average elapsed time between all recaptures was 342 days. The average time of the shortest periods between recaptures of each tortoise was 269 days in contrast with 797 days as the average time of the longest period between recaptures. The longest period between capture and first recapture extended from November 25, 1937, to February 10, 1946. The average time between the first capture and the last recapture was about 1525 days.

At least 17 of the tortoises showed signs or had records of having been in previous captivity at one time or another, probably at service stations or sheepherder camps. Five of them have holes bored in a marginal, presumably for the purpose of tethering the tortoise.

Two of them had initials carved on the scutes. Tortoise ap♂ had CR carved on second right costal scute 6. Tortoise v♂ had the initials CR carved on the second vertebral scute B and the date 1932 on scute C on January 18, 1941, but by December 8, 1945, the initials were not observable and the date had worn so that it read 1132.

Four tortoises, d♀, a♂, Cq♂ and B7♂, were all retrieved from persons who had gathered them from our study area, three of them from service station operators on U. S. Highway 91 who were commercializing the tortoises and one from a sheepherder.

Seven tortoises gathered from other sources and held in captivity at Dixie Junior College have been released on the area to see if they would remain. These include tortoises DF♀, D1♂, 2h♀, 1p♀, 1q♀, 1r and 1s. Of these, D1♂ has often been recaptured and 1s was found dead. The rest have not been seen since release.

Measurements, Weights and Temperatures

Measurement of shells was attempted in the early part of the work but the difficulty of making ac-

curate measurements led to its suspension until a better measuring device could be obtained. In March, 1943, a caliper was made from a meter stick with two right angled arms, one of which was movable, but even this had a margin of error of one millimeter. A greater source of error arose from the difficulty when remeasuring tortoises of duplicating the conditions of measurement, often resulting in errors of several millimeters.

Attempts to take weights of tortoises were made during the winter of 1938-39, but the practice was later abandoned because of its impracticability under field conditions. Weights before and after hibernation were found to vary a great deal and were felt to be unreliable because of inaccuracies resulting from voiding of feces or urinary wastes. See Table 2.

Temperatures of tortoises were taken at various times by means of a mercury thermometer inserted in the cloaca. They were taken mainly to correlate body temperatures with those of the environment and to establish the temperatures under which they were living. In addition, thermograph records were taken on weekly charts both in and out of dens, during the winter and spring of 1946. See Figure 20.

REMOVING TORTOISES FROM DENS

Removing tortoises from the dens presented great difficulties. The solution was approached from four ways. The first was the problem of illumination in the dark tunnels of the dens. Flashlights were used for most of the work, and were particularly valuable within the den, but an electric lantern was useful for general purposes of inspection. A mirror for reflecting sunlight into the openings proved useful under some conditions, but was ineffective on cloudy days, at inappropriate angles of reflection, and in crooked dens.

Second was the problem of reaching the tortoises. The tunnels ranged in length from a few feet up to 30 feet and many were irregularly curved or branched. This required personal entrance if dens were to be completely investigated. This in turn required enlargement of the tunnels. Shovels usually proved ineffective beyond the entrance. A hoe head, interchangeable with the hook of the apparatus next to be described proved most useful. With it, the dirt in the bottom of the tunnels could be scraped out deep enough to admit a person in a prone position. This was very slow work and only a few dens per year were cleared to permit complete exploration.

Third was the problem of pulling distant tortoises within reach. A wire hooked at the distal end, although useful, was very inefficient. When hooked under the edge of the open part of a tortoise shell, it would slip out of position very easily, largely because the hook was not sharp enough and the wire was too flexible. As a substitute, sections of ½ inch metal pipe about 3⅓ feet long, fitted with sleeves and carried in the trunk of the car were fitted together as needed in the field to reach various distances into the dens. A steel rod with a sharp hook about two inches long was welded to a sleeve and screwed on the end of the pipe. This was usually hooked under the pygal plate and the tortoise pulled out backward. It was very effective.

Fourth was the problem of crawling into the den. Nearly all of the dens had piles of pack rat material in them. These piles nearly always included pieces of cactus stems with spines. When scraped out, spines usually littered the bottom of the passageway over which the investigator had to crawl to enter the den. Often legs, arms and body were deeply pricked or badly scratched in the process. It was found that a narrow canvas or oilcloth rolled out in front of a person saved much of such discomfort.

RECORDS

The records include a map and a series of field notes from which all other records are compiled. These field notes were usually made in duplicate in the field and thus provided each of the authors with a set.

From these were compiled the following: a list of trips and the personnel of the parties; an index to the tortoises giving the identification of each and the successive dates on which each one was encountered; an individual record for each tortoise giving available data chronologically; maps showing the individual's home range (Figs. 22, 23).

The map was made in the field by plane table triangulation from the U. S. public survey corners aided by U. S. aerial photographs of the area. Later it was superposed on an aerial photograph enlargement for duplication (Fig. 25).

The records show that 90 trips were made to the study area between November 27, 1936, and May 1, 1946. These trips lasted from one to four days in duration and averaged about 38 days apart. They represent nearly 300 man-days of study in the area.

TORTOISE CHARACTERS

CLASSIFICATION

Order *Testudinata*.—Body shaped by a "shell" of bone and skin, usually bearing horny scales (plates or scutes), into which, head, legs and tail are retractable; limb girdles inside the ribs (shell); jaws have no teeth but are covered with horny plates which are more or less serrated and form cutting edges.

Family *Testudinidae*.—Plastron contains 9 bones; shell covered with large horny plates (scutes); plates of plastral bridge in direct contact with marginals. Contains about 20 genera and 110 species, of which, 9 genera and 33 species occur in United States.

Genus *Gopherus*.—Contains 3 species in North America; slow plodding burrowing forms; feet adapted for digging; hind feet elephant-like. True (1882:447) characterized the genus *Xerobates*, now *Gopherus*, as follows:

> "Terrestrial; horizontal alveolar surface of the upper jaw with two ridges; an interval at the symphysis, occupied by a transverse ridge; a notch in the lower jaw fitting over the transverse ridge. Anterior extremities more or less compressed in the antero-posterior direction; posterior extremities clavate; nails 5:4."

It has been shown by Bogert and Oliver (1945:399, pl. 37) that "the angle of the alveolar ridges of the upper jaw in each species is relatively constant and characteristic," but they do not give any figures to indicate the angular range in each.

Species *Gopherus agassizii* (Cooper) 1861.—A detailed description of certain external characters of this species was given by True (1882:437-440). He indicated that the chief differences between the three species were found in the shape, size or proportions of carapace, legs, inguinal scutes, head and jaws.

He separated *G. berlandieri* from the others partly by the character "shell less than twice as long as high." Bogert & Oliver (op. cit.) reported this statement not quite accurate for 13 tortoises from Texas and Coahuila, which showed ratios of .48 (.45–.57) for shell depth and plastron length, but they do not give figures for carapace length in relation to depth and hence their figures cannot be used to check True's statement which was based upon carapace length.

Of 6 tortoises from southern Texas obtained from Gordon Gunter, five which were measured, showed ratios of .506 (.47–.557) for shell depth and carapace length. Two of the five do not fall within the limits of True's statement. Comparison of the 6 specimens from southern Texas with the local Utah specimens of *agassizii* reveal some striking visual differences that are not easily described.

The Texas specimens appear dome-shaped in contrast with the flat-topped contour of the others. The adults are much smaller, ranging from 155 to 184 mm. in length whereas Utah adults range from 235 to 309 mm. The legs are smaller and more delicate, especially the hind legs which are much less elephantine in character. There also apears to be a characteristic difference in behavior difficult to describe.

There are many more points of resemblance between *agassizii* and *polyphemus* than between either of these and *berlandieri*. Both tend toward the flat-topped contour, both lay spherical eggs and both dig burrows. These, as well as many lesser morphological resemblances, are in contrast with the dome-shape, elliptical eggs (Bogert & Oliver, 1945:400) and non-burrowing habits of *berlandieri*. This latter characteristic, which was assumed by True and supported by Bogert & Oliver was further corroborated by Gordon Gunter (letter, 1946) who supplied the specimens from Texas. We concur in Bogert & Oliver's opinion that three distinct species are represented, the two showing the greatest affinities being separated in their ranges by the third which is most distinct.

The following key will assist in distinguishing them.

Carapace dome-shaped, rounded on top; carapace length about twice shell height; ratio varies from .47 to .56.

Berlandier's Tortoise *Gopherus berlandieri*

Carapace with flat-topped contour; carapace length more than twice shell height; ratio varies from .36 to .48

Hind legs large, elephantine in adult; spacing between front claws about equal to spacing of hind claws; inner surface of forearm with few or no greatly enlarged scales. Desert Tortoise *Gopherus agassizii*

Hind legs smaller, less elephantine in adults; spacing between front claws much wider than spacing of hind claws; inner surface of forearm generally bears some greatly enlarged scales.

Gopher Tortoise *Gopherus polyphemus*

WEIGHTS AND MEASUREMENTS

During the progress of this study, 41 tortoises were weighed, of which eleven were re-weighed at a later date and two others were weighed three times. The weights and lengths of these tortoises are given in Table 1 and graphs demonstrating correlations are shown in Figure 12.

The increase in weights may be the result of (a) growth, (b) food ingestion or (c) fat storage. Losses in weight result from (a) food utilization, (b) fecal elimination, (c) voiding of urine, (d) loss of carbon dioxide and water vapor from the lungs, (e) egg deposition by females and (f) loss of parts to predators. For these reasons, the graphs and correlations give only general features and not the individual factors.

TABLE 1. Weight-length relationships of tortoises from the Beaver Dam slope in Utah.

Tortoise	Date	Length mm.	Weight gm.	Date	Weight	Change
ABC♂	11- 5-38	229	2229			
B♂	11- 5-38	206	1672	2-18-39	1651	– 21
B2♀	11-30-40	. . .	1119			
B6♂	11- 5-38	274	3540			
B7♂	11- 5-38	293	3665	2-18-39	3533	–132
Be♂	11- 5-38	270	3360	10-19-40	3311.8	– 48.2
Bg♂	11- 5-38	275	3972	10-19-40	3898.7	– 73.3
Bo♂	11- 5-38	285	4090	2-18-39	4024	– 66
Bp♀	11- 5-38	250	3133	2-18-39	3046	– 87
C♀	11- 5-38	228	2305	2-18-39	2180	–125
Ci♀	11-30-40	. . .	840			
1♀	11- 5-38	263	3024	2-18-39	2956	– 68
2♀	11- 5-38	216	1873	2-18-39	1850	– 23
1e♀	10-19-40	. . .	2800	11-30-40	2618.1	–181.9
3♀	11- 5-38	223	2132	2-18-39	1990	–140
7♀	11- 5-38	204	1829			
8♂	11- 5-38	258	3237			
a♂	11- 5-38	292	3950	11- 9-40	4570.8	+620.8
a1♀	2-18-39	232	2696			
am♂	2-18-39	263	3265			
an♂	2-18-39	286	3541			
ao♂	2-18-39	288	3382			
ap♂	2-18-39	262	3009			
aq♀	2-18-39	200	1699			
ar♂	2-18-39	212	1649			
b♀	11- 5-38	213	1760			
c♂	11- 5-38	248	2358.5			
d♀	11- 5-38	153	722			
e♂	11- 5-38	178	1083			
f♂	11- 5-38	280	4190			
g♂	11- 5-38	279	4093			
h♂	11- 5-38	286	5228.5			
i♂	11- 5-38	223	2036			
j♂	11- 5-38	267	3735			
k♂	11- 5-38	273	3812	10-20-40	3845.6	+ 33.6
Un-branded						
♂	3-31-46	305	5220			
♂	3-31-46	262	3920			
♂	3-31-46	280	3886			
♂	3-31-46	267	3692			
♂	3-31-46	256	2895			
♀	3-31-46	210	1835			

TABLE 2. Length, width, and height measurements, and ratios of 117 tortoises from Beaver Dam Slope, Utah.

No. and Sex	Date	Length mm	Width at do	Height	Ratios: Width / Length	Ratios: Height / Length
ABC♂	11- 5-38	229				
	3- 4-44	237	174	103	.735	.435
	10-20-45	241	174	104	.722	.432
	1-19-46	242	173	110	.715	.455
A8♂	2-20-44	251	191	110	.761	.438
	12- 2-45	253	191	112	.756	.443
Ah♂	1-22-44	285	228	137	.801	.481
	12- 8-45	289	230	130	.796	.450
Am♂	3- 4-44	266	212	114	.797	.429
An♂	12- 2-45	269	213	118	.792	.439
Ap♂	3- 4-44	304	231	123	.760	.405
	12- 2-45	305	229	122	.752	.401
At♂	12- 2-45	247	178	109	.721	.442
B♂	11- 5-38	206				
	3-19-43	302	209	122	.693	.401
	1-13-45	299	206	116	.689	.389
B6♂	11- 5-38	274				
	3-19-43	277	209	119	.729	.415
	9-18-43	268	217	121	.800	.452
	2-20-44	269	213	117	.792	.435
	1-19-46	274	209	122	.737	.430
B7♂	11- 5-38	293				
	3-19-43	298	207	...	.697	
	3- 4-44	295	206	113	.700	.382
	11-17-45	299	207	111	.693	.372
	1-27-46	298	206	117	.692	.393
Be♂	11- 5-38	270				
	3- 4-44	265	199	110	.752	.416
	1-13-45	268	199	109	.743	.407
	11- 4-45	267	195	112	.730	.419
Bg♂	11- 5-38	275				
	2-10-46	273	206	121	.756	.444
Bh♂	1-22-44	278	206	118	.741	.425
Bk♂	10-31-43	285	213	120	.748	.421
	1-28-45	289	213	121	.737	.419
	10-28-45	283	213	119	.753	.422
	3- 2-46	289	213	114	.738	.395
Bm♂	10-28-45	245	182	107	.742	.436
	11- 4-45	245	182	104	.742	.425
Bs♂	10- 2-43	268	212	118	.792	.441
	1-28-45	275	216	127	.785	.462
	10-28-45	271	210	126	.775	.465
C2♂	1-22-44	263	194	123	.737	.468
	11- 4-45	265	197	119	.742	.448
C5♂	3-19-43	250	190	105	.760	.420
	2-20-44	250	189	108	.757	.432
	10-20-45	253	191	104	.750	.412
C6♂	2-20-44	262	194	114	.740	.435
	11-17-45	266	191	117	.718	.440
Cg♂	5-27-44	247	174	101	.704	.408
	1-28-45	248	177	108	.714	.440
	11- 4-45	247	178	99	.721	.401
Cj♂	3-19-43	275	195	114	.710	.415
	11-28-43	273	196	121	.718	.443
	1-13-45	276	194	114	.703	.413
	10-20-45	275	196	120	.713	.437
	2- 3-46	275	195	120	.709	.437
Cl♂	10-31-43	262	196	118	.749	.450
	1-28-45	268	196	119	.732	.444
	10-28-45	267	195	122	.731	.457
	11- 4-45	267	195	122	.731	.457
Cn♂	3-19-43	260	185	109	.712	.420
	11-28-43	255	185	107	.726	.419
	10-20-45	257	186	107	.724	.416
	1-19-46	256	183	107	.732	.418
Cr♂	1-22-44	309	230	144	.745	.466

TABLE 2. (Continued)

No. and Sex	Date	Length mm	Width at do	Height	Ratios: Width / Length	Ratios: Height / Length
Cv♂	12- 2-45	281	219	113	.780	.403
Dl♂	4- 9-42	278	214	...	.770	
	3-19-43	278	206	...	.741	
	9-18-43	275	209	122	.760	.444
	11-28-43	271	202	121	.745	.447
	1-13-45	277	206	122	.745	.441
	10-20-45	278	207	123	.745	.443
D2♂	10-20-45	297	210	113	.709	.381
	1-19-46	296	209	108	.706	.365
D6♂	1-19-46	278	207	120	.745	.432
D7♂	3-20-43	287	216	113	.753	.394
	3- 4-44	287	217	112	.757	.391
	12- 8-45	286	214	117	.749	.410
E♂	5-15-43	263	200	117	.761	.445
	5-27-44	266	199	119	.750	.448
	11-17-45	269	194	118	.721	.439
EF♂	2-10-46	276	191	110	.693	.399
F7♂	2-10-46	285	204	114	.716	.400
F8♂	2-10-46	257	184	112	.717	.436
Fi♂	2-10-46	285	204	120	.716	.467
Fj♂	2-10-46	316	230	134	.728	.424
le♂	10- 3-43	248	179	103	.722	.415
	10-31-43	248	179	105	.722	.423
li♂	3-19-43	260	199	113	.768	.435
	2-20-44	256	200	110	.782	.430
	1-19-46	257	199	120	.775	.467
lk♂	3- 4-44	271	199	116	.736	.428
	12- 8-45	274	197	120	.719	.438
lu♂	5-27-44	260	189	106	.727	.407
	11- 4-45	264	192	108	.726	.408
lv♂	11- 4-45	230	172	98	.747	.425
23♂	10-31-43	252	190	107	.755	.425
24♂	10-31-43	259	187	114	.720	.440
	1-28-45	264	189	115	.716	.436
	10-28-45	263	189	114	.718	.433
2d♂	1-19-46	288	208	119	.723	.414
ac♂	3-19-43	264	205	120	.777	.455
	2-20-44	263	204	116	.776	.441
	1-19-46	264	202	118	.765	.447
ad♂	3-19-43	260	205	116	.790	.447
	1-19-46	259	204	116	.789	.448
ae♂	1-13-45	267	203	120	.760	.450
ah♂	3-19-43	266	187	102	.703	.384
	2-20-44	266	188	104	.707	.391
	1-19-46	266	186	108	.700	.406
ai♂	12- 2-45	228	173	94	.760	.412
am♂	2-18-39	263				
	12- 2-45	276	211	115	.764	.417
an♂	2-18-39	286				
	2-20-44	288	201	115	.700	.400
	12- 2-45	290	200	116	.690	.400
ap♂	2-18-39	262				
	2-20-44	264	195	113	.740	.428
f♂	11- 5-38	280				
	2-18-39	283				
	10-20-45	284	223	123	.785	.433
	2- 3-46	283	223	125	.788	.435
g♂	11- 5-38	279				
	3-19-43	276	211	125	.766	.453
	11-28-43	266	209	128	.786	.467
	10-20-45	274	209	127	.763	.464
	1-27-46	273	210	128	.770	.469
h♂	11- 5-38	286				
	3-19-43	288	232	123	.806	.427
	5-27-44	290	230	129	.794	.445
i♂	11- 5-38	223				
	3-11-39	223				

TABLE 2. (Continued)

No. and Sex	Date	Length mm	Width at do	Height	Ratios	
					Width Length	Height Length
j♂	11- 5-38	267				
	3-19-43	278	201	112	.723	.403
	1-13-45	278	200	117	.720	.421
	11-17-45	281	198	115	.706	.410
	1-19-46	281	198	114	.705	.406
k♂	11- 5-38	273				
	3-19-43	277	210	114	.760	.412
	11-28-43	273	208	111	.763	.407
	1-13-45	278	208	116	.748	.418
lu♂	10-20-45	281	215	118	.765	.420
r♂	2-20-44	264	190	107	.720	.405
v♂	3-20-43	286	203	116	.710	.406
	3- 4-44	286	203	116	.710	.406
	12- 8-45	284	204	117	.718	.412
Un-branded						
♂	3-31-46	305	215	119	.705	.391
♂	3-31-46	262	202	117	.772	.447
♂	3-31-46	280	202	117	.730	.418
♂	3-31-46	267	189	113	.708	.424
♂	3-31-46	256	176	102	.688	.399
AF♀	1-28-45	258	182	110	.706	.426
A1♀	11-28-43	211	153	90	.726	.427
A6♀	3- 4-44	236	176	101	.746	.428
	12- 2-45	239	180	103	.753	.430
B5♀	10- 3-43	215	164	81	.763	.376
B8♀	1-22-44	272	201	112	.740	.412
	1-13-45	273	204	123	.747	
	12- 8-45	271	201	107	.743	.394
Bb♀	1-13-45	247	185	109	.749	.441
	11- 4-45	247	187	106	.767	.429
Bd♀	2-20-44	251	192	105	.765	.418
	10-20-45	256	190	107	.742	.418
	2- 3-46	254	190	109	.748	.431
Bdo♀	2-18-39	228				
	2-20-44	233	180	97	.772	.415
Bf♀	10-20-45	231	175	101	.758	.437
Bfq♀	11-28-43	228	173	95	.760	.416
	1-13-45	232	173	102	.746	.435
	10-20-45	230	170	97	.740	.422
	1-27-46	227	164	95	.723	.418
Bgr♀	5-27-44	237	169	97	.714	.409
Bj♀	1-22-44	217	155	91	.715	.419
Bl♀	10-31-43	257	187	110	.729	.429
	1-28-45	258	190	111	.738	.464
	10-28-45	261	192	112	.737	.430
Bp♀	11- 5-38	250				
	3-19-43	253	189	...	.748	
	9-18-43	251	193	113	.770	.445
	11-17-45	248	190	110	.766	.444
Bq♀	3- 4-44	242	176	97	.728	.401
	12- 8-45	240	173	95	.721	.393
C♀	10-28-38	228				
	3- 4-44	232	174	95	.751	.427
	5-27-44	231	171	96	.740	.435
	1-13-45	229	173	95	.756	.418
	1-28-45	231	172	95	.745	.414
CE♀	10-31-43	226	163	98	.715	.434
	1-28-45	232	166	96	.715	.413
	10-28-45	237	171	99	.721	.417
C7♀	10-20-45	211	157	89	.745	.421
	1-27-46	209	156	90	.746	.430
Ca♀	1-28-45	257	188	107	.732	.417
Cb♀	10- 3-43	240	188	100	.783	.417
Cc♀	5-27-44	224	163	95	.728	.423
Cd♀	3-19-43	238	171	96	.717	.403
	11-17-45	235	168	95	.714	.403
Ce♀	10-28-45	237	171	99	.720	.417
DE6♀	12- 2-45	283	210	116	.741	.410
D4♀	11-17-45	225	167	94	.742	.417
D4c♀	1-28-45	265	191	107	.722	.403
	10-28-45	264	191	110	.723	.417
Dj♀	1-28-45	263	193	110	.733	.418
	2-10-46	261	192	109	.735	.417
E7♀	12- 2-45	192	139	82	.723	.427
E8♀	1-19-46	207	150	89	.723	.429
F4♀	1-19-46	245	174	97.5	.710	.397
F5♀	1-19-46	245	176	94	.718	.383
F6♀	1-27-46	170	127	75	.746	.441
Ff♀	2-10-46	231	161	101	.697	.436
1♀	11- 5-38	263				
	3-19-43	258	185	105	.718	.407
	11-28-43	256	181	104	.708	.406
1a♀	2-20-44	269	198	113	.735	.421
	12- 2-45	264	198	116	.750	.438
1b♀	1-28-45	221	161	91	.730	.410
1c♀	10-31-43	243	173	100	.713	.412
	1-28-45	246	173	100	.703	.407
	10-28-45	246	174	102	.708	.411
1d♀	3-19-43	203	150	86	.738	.423
1e♀	1-13-45	245	186	114	.760	.465
1l♀	1-13-45	197	144	75	.730	.380
1n♀	1-13-45	227	172	98	.756	.432
1t♀	11- 4-45	216	153	88	.708	.407
7♀	11- 5-38	204				
	9-18-43	234	180	102	.770	.437
	11- 4-45	239	179	106	.750	.443
8♀	11- 5-38	258				
	10-28-45	261	197	118	.755	.453
al♀	2-18-39	232				
	2-20-44	243	179	99	.736	.407
	12- 2-45	242	175	99	.722	.409
au♀	4- 9-42	262	199	...	.760	
lo♀	3-19-43	234	177	89	.756	.380
	1-13-45	234	176	86	.752	.367
	10-20-45	236	177	84	.749	.356
	1-19-46	234	176	84	.752	.358
o♀	1-28-45	301	212	117	.703	.388
	10-28-45	293	211	120	.719	.408
s♀	3-19-43	250	177	...	.708	
	3- 4-44	249	179	100	.720	.402
	1-13-45	249	177	99	.710	.398
	10-20-45	251	177	102	.706	.407
	11-17-45	249	176	98	.706	.394
Un-branded						
♀	3-31-46	210	156	90	.742	.428

Measurements.—Measurements of 117 tortoises were made in which the carapace length along the midline, the width across the centers of the fourth marginals and the vertical depth of body at a point between the second and third vertebrals were recorded. All measurements were made with calipers in planes parallel to or at right angles with the flat surface upon which the tortoise was resting. These tortoises were measured from one to six times each. Table 2 gives measurements and ratios from which size, form and growth may be computed.

The height-length and width-length ratios have been computed. The height-length ratios derived from 132 measurements of 64 males ranges from .365 to .481 and those from 83 measurements of 49 females from .356 to .465. The width-length ratios (width at

do) derived from 136 measurements of 64 males range from .688 to .806 and those from 86 measurements of 50 females from .703 to .783.

EXTERIOR AND SHELL

The desert tortoise is mainly brown horn color, often lighter below and around the edges of the exposed marginals. Sometimes there is an inconspicuous darker band around the carapace and often the dorsal plates have darker centers. There is a great deal of variation in the arrangement of the darker and lighter areas.

The shell is longer than wide and wider than high. The plastral bridge is strong and the anterior and posterior plastral projections are not hinged and cannot be closed. Instead, the limbs are adapted to fill the openings. When fully retracted, the anterior opening is completely filled by the front forelegs. The posterior opening is filled by the tail, the proximal parts of the thighs and the bottoms of the elephant-like feet.

The shell normally contains 37 plates or scutes on the carapace and 16 on the plastron, arranged as shown in Figures 4 and 5. Those of the carapace include a central row of 5 vertebrals bordered on each side by a row of 4 costals, all of which are surrounded by a single row of plates around the edge. This single row includes 11 marginals on each of the right and left edges which are separated by the nuchal in front and the pygal behind. The plastron contains 6 pairs of large paired scutes, which are in contact along the mid-ventral line. Beginning in front, these are known as gular, humeral, pectoral, abdominal, femoral and anal plates. There are additional small paired scutes not in contact which are known as the axillary and inguinal on the anterior and posterior edges of the bridge, respectively. Grant (1944:114) has called attention to asymmetry of the mid-ventral suture between the pair of gular scutes in which the left is wider at the base than the right, thus causing a deviation of the midline (see p. 156).

The movable parts of the body—the head, the legs and the tail—bear smaller scales which are larger, stronger and often sharply pointed on the portions exposed when retracted, but which are smaller, weaker and often obsolete on those portions that are protected. Thus the animal, when head, legs and tail are retracted within the shell, offers a formidable defense against predators. The whole exterior is covered by a continuous expanse of horny plates or heavy sharp-pointed scales on the legs. In this condition, if touched, the legs are rigidly held in the shell openings, thus offering the maximum "passive resistance" to a predator.

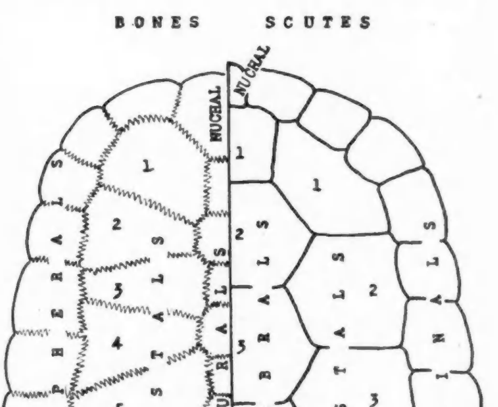


FIG. 4. Sketch of typical carapace showing relation of the underlying bones to the overlying scutes.

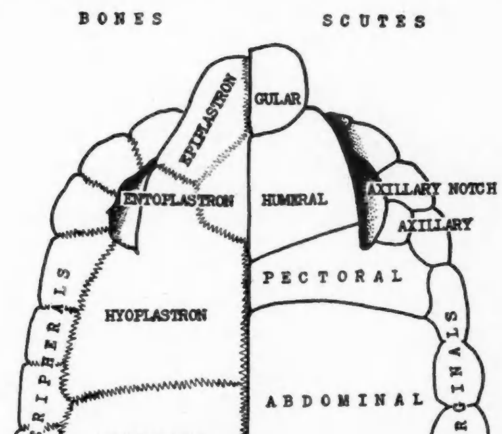


FIG. 5. Sketch of typical plastron showing relation of the underlying bones to the overlying scutes.

SKELETON

The bones of the shell underlying the scutes differ in form, number and arrangement from the scutes as shown in Figures 4 and 5. The shell normally contains 50 bones in the carapace and 9 in the plastron.

Those of the carapace include a central row of bones which normally contains one nuchal, 8 neurals, 2 suprapygals and one pygal; a lateral row of 8 costals on each side and a single row of 11 peripherals on each edge. These two rows of peripherals are separated in front by the nuchal and behind by the pygal. The plastron contains one single bone, the entoplastron, and 4 pairs of bones; the epiplastrons, the hyoplastrons, the hypoplastrons and the xiphiplastrons. The hyo- and hypoplastrons normally connect with the peripherals to form the bridge.

The 8 neurals are fused with the flattened neural spines of numbers 2 to 9 of the 12 dorsal vertebrae. The neural spine of the first of the dorsal vertebrae flattens out against the first neural and the spine of the second fuses with the same neural bone. The third spine fuses with the second neural, the fourth with the third and so on to the ninth spine which fuses with the eighth neural bone. The spines of the last three dorsal vertebrae are free.

The second pair of ribs extending from the first and second dorsal vertebrae fuses with the first pair of costal plates. The first pair of ribs extending from the last cervical and first dorsal vertebrae joins and fuses with the second pair where they flatten out on the costal plates. The third to eighth pairs of ribs each of which connect with two vertebrae, except the eighth, fuse with the second to seventh neurals, respectively, which are separated from the costals by sutures. The ninth and tenth pairs extending from the ninth and tenth vertebrae, respectively, pass by the neurals and fuse with the last (eighth) pair of costals beyond the sutures. The sacral ribs extending from the center of the eleventh and twelfth vertebrae unite at their distal ends and attach to the dorsal ends of the ilia of the pelvic girdle. A process from each of the tenth ribs at its point of fusion with the costal plate is attached to the distal end of each of the first sacral ribs which extend from the eleventh vertebrae to the point where they join the ilia, thus anchoring the pelvic girdle to the shell.

On those costal plates adjacent to neurals 2 to 7, there is a thickening that forms a slight ridge which appears to be an extension of the rib distal to that which fused with the neural but is now separated by the neural-costal suture. Costal plate numbers 2, 4 and 7 are each in contact with one neural only. Numbers 1, 6 and 8 are each in contact with 2 neurals. Numbers 3 and 5 each contact 3 neurals. Those costals which are in contact with one neural usually expand distally to contact more than one peripheral, whereas those which contact 3 neurals usually contract distally.

Eight of the dorsal vertebrae, nos. 2 to 9, are fused to the shell, but numbers 1, 10, 11 and 12 and the caudal and cervical vertebrae are free. The caudal vertebrae vary in number; two males each had 18, the last one being vestigial and one female had 11. The last cervical vertebra has a very free vertical articulation with the first dorsal vertebra which allows the head to be withdrawn into the body through the opening of the pectoral girdle.

There is great variation in the articulations between the various cervical vertebrae, the posterior ones being mainly limited to vertical movements while the anterior permit considerable lateral movement. These attach in the usual manner of the *Testudinidae* to the skull, the dorsal arrangement of which is shown in Figure 6.

The pectoral girdle shown in Figure 6, is set inside the shell. The principal bones of the girdle, shaped like a pair of parentheses, are attached at their dorsal ends to the first costal plates on each side of the first vertebra. The ventral ends attach to the entoplastron. These parentheses-shaped bones constitute the scapulae and their projections, the prescapular processes (Hyman 1942:146). The coracoid, a large flattened blade-shaped bone, joins the scapula at the glenoid fossa and projects ventro-caudally toward the hyoplastron.

The humerus, extending from the glenoid fossa is strongly curved downward and articulates at a right angle with the axis of the bone on its ventral surface with the radius and ulna. The arrangement of the bones of the forelimb is illustrated in Figure 6. It is interesting to note the fusion of the radiale with centrale and carpel one with carpel two. Digit 5 contains only one phalange whereas each of the other digits has two.

The pelvic girdle, shown in Figure 6, is anchored inside the shell, the dorsal ends to the last costals as already explained. On the ventral side, the ischia attach to the xiphiplastron and each lateral pubic process is attached to the adjacent hypoplastron.

The femur, extending from the acetabulum, is slightly curved downward and articulates at a right angle to its axis on its distal ventral surface with the tibia and fibula. The arrangement of the bones of the hind limb is shown in Figure 6. The upper tarsals are fused into one piece which represents the tibiale, fibulare, intermedium and centrale. Tarsals 1 and 2 are fused. A large metatarsal enclosed in the foot is the only remnant of digit one. The other digits have only 2 phalanges each.

INTERNAL SYSTEMS

If the plastron be removed by sawing across the bridges, the internal systems of the coelom will be exposed (Figs. 7 and 8). Posterior to the bend of the neck when retracted, lies the heart in the pericardial cavity. This consists of a large triangular ventricle fastened by a ligament at its ventral end and attached to the two auricles dorsally by a narrow constricted attachment. The arterial trunk leaves the ventricle anteriorly without any attachment to the auricles.

The liver consists of two lobes connected by a narrow bridge, one lobe on each side of the pericardium. The right lobe which fits the interior of the shell behind the front legs, contains a large gall bladder

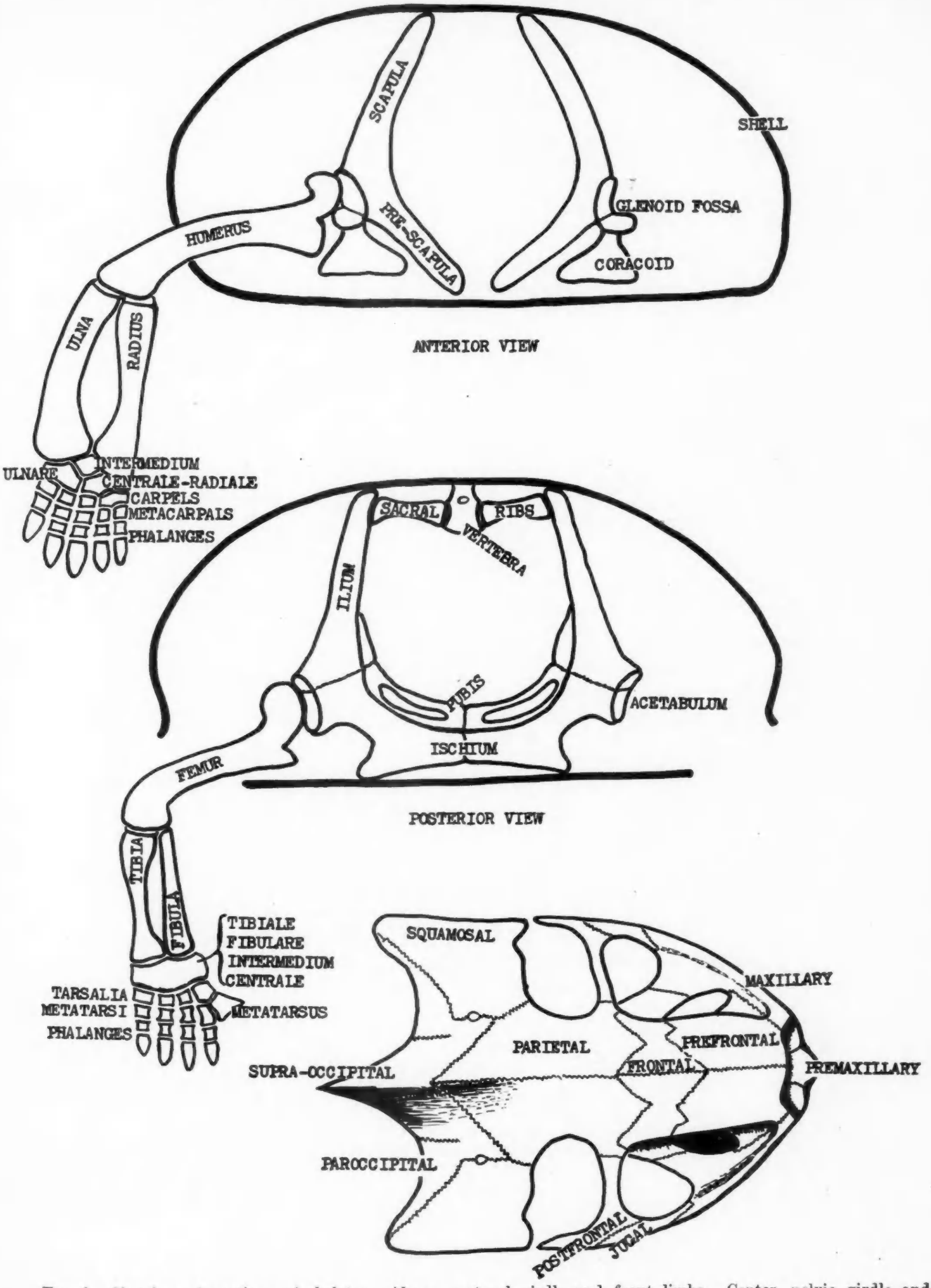


FIG. 6. Sketches of portions of skeleton. Above, pectoral girdle and front limbs. Center, pelvic girdle and hind limbs. Below, dorsal view of skull.

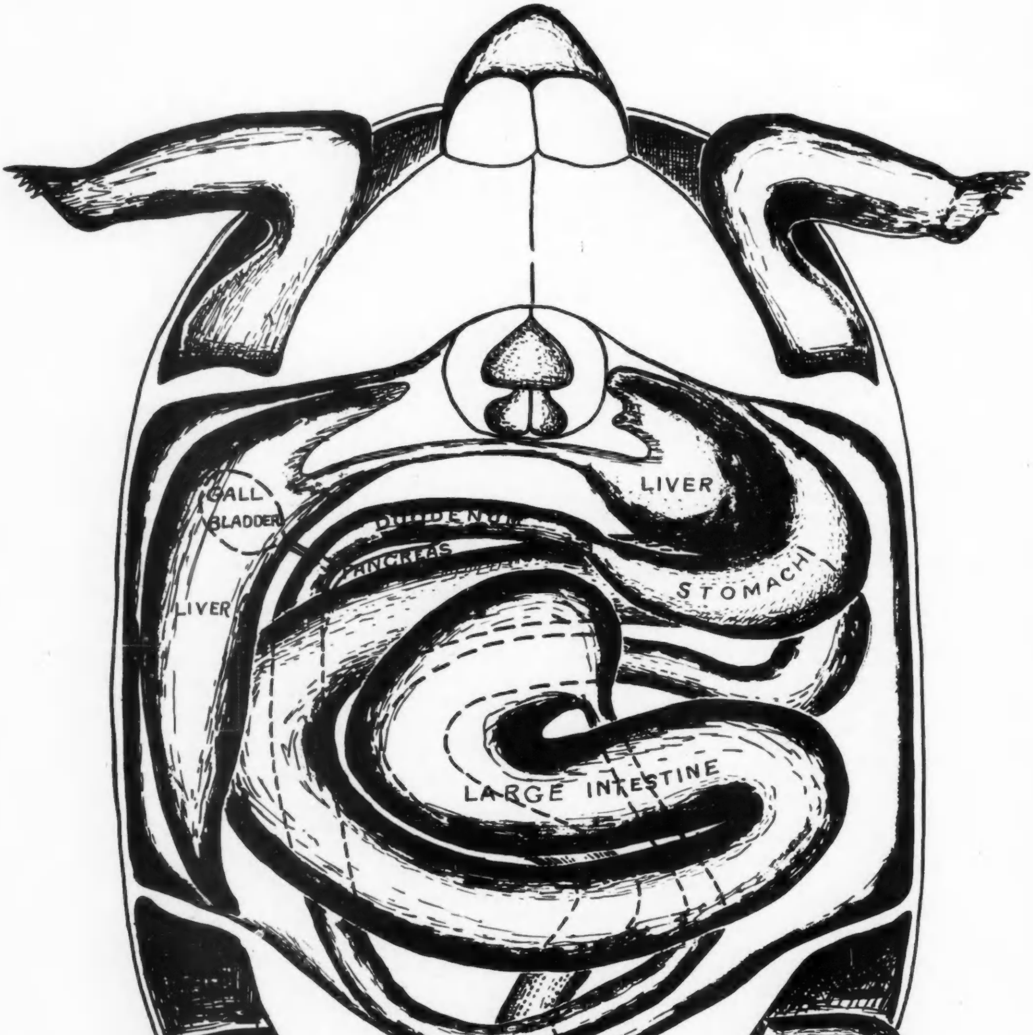


FIG. 7. Sketch showing arrangement of digestive system.

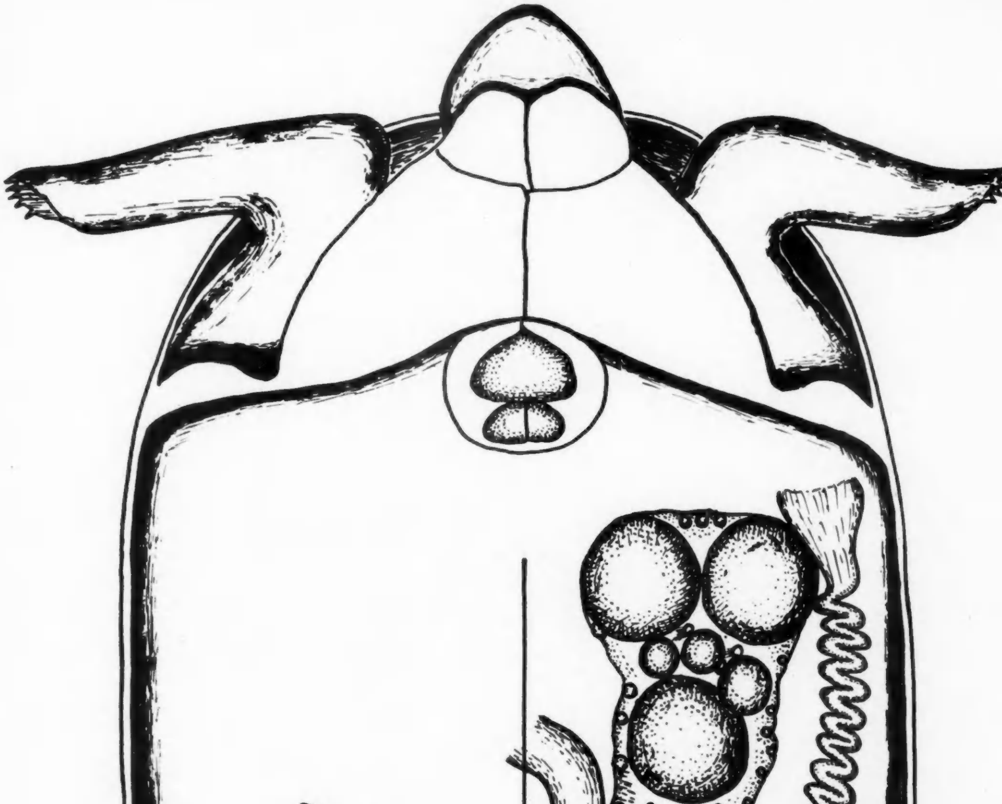


FIG. 8. Sketch showing arrangement of urogenital system.

which connects by means of the bile duct, about 25 mm. in length, with the small intestine at a point about 75 mm. from the stomach. Near this point, the long slender pancreas is stretched along the inner curve of the intestine.

The esophagus leading from the mouth gives way to the stomach at the left lobe of the liver, around which it curves in a large arc. At the end of the stomach, the pyloris is scarcely noticeable where it joins the small intestine which makes a large sweep to the right side and makes a turn backward just before reaching the right lobe of the liver where the bile duct enters.

The small intestine passes backward along the right side, turns left in front of the hind legs and then passes forward toward the center of the coelom where it abruptly enlarges into the large intestine.

The large intestine running right, soon makes a reverse turn posteriorly to the left. Before reaching the left side, it makes another posterior reverse turn to the right, ventral to the small intestine which it crosses three times. At the right side it passes forward against the liver, ventral to the small intestine and makes a wide sweep to the left dorsal to the stomach where it turns posteriorly and gradually reduces its size and then turns to the right, dorsal to both the small and large intestines. From here it makes a sigmoid flexure to the cloaca.

In three cases of females dissected, the left ovary was much better developed than the right, one left ovary having three, one five and the other seven well developed yellow eggs, whereas one right ovary had one, the two others none. Each ovary is suspended from the carapace by the mesovarium. A much convoluted oviduct lies lateral to the ovary along the side. The ostium extends forward nearly to the front legs. The posterior end enlarges into a uterus. The two uteri join together externally before entering the cloaca, giving the appearance of a united structure but internally each uterus has its own sphincter (Fig. 8).

Inside the ventral wall of the female cloaca, is a small rounded double structure, the clitoris, which is the female equivalent of the male penis. The testes are elongated brown bodies suspended in the posterior coelom on each side of the midline by the mesorchium which separates each testis from the respective kidney lying behind the peritoneum against the posterior body wall. Lying next to each testis is an epididymis which consists of a much coiled tube enclosed in a transparent membrane. It connects with the cloaca exteriorly just anterior to the bladder but the short vas deferens opens interiorly into the anterior end of the urethral groove at the base of the penis.

Lying inside the ventral wall of the cloaca, are two long slender rod-like bodies, the *corpora cavernosa*, each of which has a bulb at its anterior end and both of which are joined together in a heart-shaped body, the glans, at the posterior end. When at rest the rod-like bodies make a bend near the bulbs and project forward, bulging the wall of the cloaca into the coelom. When excited, they enlarge and straighten, thrusting the penis out the cloacal opening.

The flattened, rounded dark or reddish brown kidneys lying behind the peritoneum in the dorso-posterior region drain through separate ureters along the dorsal side of the epididymis and empty into the neck of the bladder. The large bi-lobed urinary bladder lying in the ventro-posterior part of the coelom connects with the cloaca posterior to the ureter entrance by means of a short stalk which appears to have a valve in it. The bladder usually contains a large amount of water and great quantities of the whitish precipitate of uric acid. The accessory bladders which are described (Hyman 1942:407) as elongated sacs for other turtles, are here reduced to small pouches probably with little functional value.

Lying on the side of the kidney between it and the peritoneum separating it from the epididymis is a rich brown flattened body, the suprarenal gland.

The two lungs lying between the peritoneum and the carapace and extending backward nearly to the kidneys, are spread out flat and thin, but are, of course, expandible. The lateral edges project outward in five small lobes. When a tortoise is on its back, the weight of the internal systems would rest upon the lungs and make it difficult for a tortoise to breathe normally. It is conceivable that long-concontinued pressure in such a position would cause death by suffocation. The trachea and its two branches, the bronchial tubes may be observed traversing the neck when the heart is removed.

VARIATIONS

Among the characters of the family *Testudinidae* given by Hay (1908:367), it is stated that: "Penultimate suprapygal usually bifurcate, with its limbs resting on the hinder peripherals and enclosing the hindermost suprapygal." While this typical condition is found in some shells, there is a great deal of variation in this arrangement. Sometimes this small enclosed posterior suprapygal is expanded until it separates the anterior suprapygal from the peripherals. Occasionally the anterior suprapygal is divided by a transverse suture to form an extra neural.

Other extra neurals may be produced by transverse sutures across the normal neurals, thus forming irregular shapes and departing from the usual tetragonal and octagonal pattern of alternates. This may increase the usual number of 8 to 9 or 10.

There are many variations in the scutes revealed in our field notes. Four tortoises had only 10 marginals on each side instead of the usual 11. In tortoise Ag♂, scutes k and v were missing, but the field notes do not indicate which are lacking on tortoises Bm♂, 23♂ and 24♂. Bg♂ had 10 marginals on the right, v being missing; and 11 on the left, but k was very small.

Each of six tortoises had an extra marginal on each side, making a total of 12. Tortoise au♂ had the two extras in front of the bridge and also had 3 additional small plates along the edge. Tortoise Cn♂ had the extras in the rear next to the pygal plate F. Tortoise Bk♂ had the extras in front of the bridge, between b and c plates on one side and

m and n on the other. This tortoise was especially wide and flat. Tortoises E7♀, 1♀ and 1t♀ all had an extra scute on each side of the nuchal, between a and l. The location of extras on tortoise 11♀ were not given.

Each of three tortoises had an extra marginal on one side only. The extra one on tortoise C7♀ was located between scutes a and d. On tortoise ag♀, it was located just left of the nuchal and on tortoise f♂, between a and e. Tortoise Cn♂ had scute l partly split, which if completed would produce an extra marginal. It also had an extra on each side of pygal scute F. Tortoise Bgr♀ has 5 marginals in front of bridge, 3 on bridge, and 5 behind bridge, making a total of 13 on each side.

In some cases, extra scutes produce peculiar irregularities. Tortoise Ca♀ and Cf♀ have two nuchals each. Tortoise v♂ has the nuchal partly fused with the first marginal scute l. Tortoise DE6♀ has an aberrant area around marginal scutes q and r that is especially peculiar. Scute q is divided, making 2 scutes, one dorsal to the other. Scute r is bordered by 3 small and one very small scutes between q and s.

There are some irregularities in the costal scutes also. Tortoise Fl has 5 right costals and tortoise h♂ has 5 left costals. Tortoise B8♀ is very unsymmetrical. She has 5 left and 3 right costal scutes as well as an extra vertebral made by transverse division of scute D and one marginal is missing by fusion of the nuchal with scute l. What should have been the first right costal has been absorbed by the first vertebral scute A and the second right costal scute 6. The first left costal has been divided.

The inguinal scutes are especially variable, ranging from one extreme of 2 equal sized scutes with a variable series of smaller ones between them to a single one with a diminishing series of smaller ones trailing from it. The midventral line of the plastron is also exceedingly variable, often being jagged and irregular as a result of offsets between different pairs of scutes as reported by Grant (see p. 155). Tortoise F4♀ shows an extreme example where the lines are not only offset at each junction, but the lines themselves slant in different directions.

An unbranded tortoise from an area about 10 miles to the northwest had a very aberrant scute arrangement. The marginals, costals 1 and 5, and vertebrals A and B were normal. Scute C was concave posteriorly to accommodate an extra scute resulting from a diagonally transverse division of scute D. Costals 3 and 7 and vertebral E were exceptionally large to occupy the space ordinarily filled by costals 4 and 8 which were missing. There was also an extra pair of scutes on the plastron enclosed between the pairs of abdominal and femoral scutes. The bones underlying these irregular scutes appeared to be normal in number and position.

BONE AND ITS REGENERATION

The origin of the bones of the shell is a problem, upon which some of our studies have a bearing. Occasionally tortoises were found on which that part of the scute enclosed within the arms of the U brand was shed, thus exposing the bone underneath. It was of much concern at first for fear of detriment to the tortoise, but later it was found to be a common natural phenomenon wherever the shell was injured.

Later, it was also discovered that the exposed bone was eventually shed, and replaced underneath by a new piece of scute which in turn rests upon a new piece of bone below it. This gradually grows into place so that the repaired part becomes indiscernible.

The mode of repair has not been studied histologically, but it seems obvious that the new piece of scute underneath the original bone must be in contact with the edge of the old scute where the repair is to be made, thus cutting through the original bone and isolating the piece to be discarded. The new bone underneath probably grows from the edge where the old piece was cut out.

Repairs of this kind appear to be made at any place on the shell, whether carapace or plastron, wherever injuries occur. This appears to support the idea that the bones of the shell are of dermal origin. Additional support comes from study of the bone itself.

The individual bones of the shell show what are believed to be ossification centers, from which, the minute ridges on the surface of the bone tend to radiate in all directions. Where the bone from one center contacts that from another center, an irregular suture occurs. The position and direction of these sutures probably depends upon the rate of growth of adjacent centers at the time the bone was laid down or upon the sequence in initiating the centers.

Where the chondral bone of the ribs or the neural spines of the vertebrae join the bones of the shell, they fuse together without sutures. This raises the question: may the costal plates be only flattened ribs? It is believed that the evidence does not warrant such a conclusion. Ribs join both neurals and costal plates, some places only one, other places both. Where the rib joins a neural, it is usually separated from its continuation along the costal plate by the neural-costal suture. This is better explained as a suture in the dermal bones than a suture across the rib. Furthermore many of the bones of the shell such as the nuchal, pygals and peripherals develop independently of the ribs or vertebrae, and appear to act in a similar way to the neurals and costals in the repair of the shell.

This repair of the bone is a very slow process. It was first noted on 1e♀ on October 19, 1940, but its significance was not discovered until February 1, 1941 on tortoises Bp♂ and e♂, 819 and 827 days, respectively, after they had first been branded on October 28, and November 5, 1938. At that time, it was noted that bone was showing in the branded scutes where the horny material of the scute had been sluffed off between the arms of the U.

Since then, it has been noted many times, both on brands and in damaged parts of the shell. Bfq♀ was branded on October 28, 1938. More than four years later (1520 days) on December 26, 1942, it was

recorded that the horn on scute q had sealed off exposing bone between the arms of the U brand, and that some of the bone had broken off exposing horn underneath the center of the bone. More than seven years (2648 days) after the original branding, it was recorded on January 27, 1946 that bone was exposed on scute f, that bone and a little regenerated horn was exposed on scute B and that a little bone with much regenerated horn was exposed on scute q.

Bone has been recorded as being exposed on brands as follows: 1e♀ had bone that was sluffing off and exposing horn underneath after a lapse of 1639 days on October 3, 1943; Cg♂ had bone on scute C but had been replaced by horn on scute g on May 27, 1944 after a lapse of 1758 days; 1u♂ had bone on scute 1 but had horn on scute u on May 27, 1944 after a a lapse of 1848 days; Dj♀ still had some bone in base of brand on February 10, 1946 after a lapse of 1919 days; Be♂ was showing new horn underneath bone on March 4, 1944 after a lapse of 1946 days; ad♂ and ah♂ both showed traces of bone mostly replaced by horn on January 19, 1946 after a lapse of 2211 days; Cn♂ had bone around edges of brand, mostly replaced by horn in center on January 19, 1946 after 2296 days; 1i♂ still had bone on scute 1, but horn had replaced most of the bone on scute i on January 19, 1946 after lapse of 2450 days; ABC♂ and j♂ both had bone on all the brands on January 19, 1946 after a lapse of 2632 days; g♂ had most of the bone replaced by horn on the brand on January 27, 1946 after a lapse of 2640 days, nearly 7¼ years.

Not all of the tortoises branded were affected in this way. Many of the brands remained intact without showing signs of regeneration, but a few became dim, probably through wearing of the surface and were rebranded when necessary as were some of those showing regeneration.

ABNORMALITIES DUE TO INJURIES

In some cases, abnormalities have resulted from injuries to the tortoises. In three cases the front feet have been damaged. F8♂ when first marked on November 25, 1937 was uninjured, but was not recaptured until February 10, 1946 when he had a left front foot with the claws and distal end missing. The right front foot had numerous small abnormal scales where an injury had healed. There was regeneration of horn on the margin of scutes c and d; at the junction of h, i, 3, and 4; on F; and at the junction of m and n. Tortoise Ce♀ showed a scar on the right front foot where the claws were missing as if they had been chewed off by a carnivore. It also had sunken areas in vertebral scutes A, B and C. Tortoise D7♂ had a scar on the right front leg where some scales were missing. This, too, looked suspiciously like the work of a carnivore. Tortoises k♂ and 8♂ appear to have had the ends of the tails removed. Tortoise lo♀ was very "sway-backed."

There are many examples of damage to the shell, in which the resulting abnormalities are gradually repaired as described under "Bone and Its Regeneration." Tortoise Co♀ had the edges of all of the front marginals chewed off back to the bridge on October 6, 1939. She has not been recaptured since that time. Tortoise Bh♂ had scutes k, E and F badly cracked on February 17, 1940, but no further reference occurs in the field notes although he has been recaptured 6 times since then. Tortoise D8♀ likewise had the shell badly cracked, affecting scutes 5, 6, o and p, but it was healed on January 18, 1941. There is no further record.

On January 1, 1941, tortoise D4♀ was reported as having had an injury that left irregular markings on scutes A, B, and 1, but there is further reference in the notes of its recapture on November 17, 1945 when the injury was again recorded with the remark that it was all broken and disfigured. Tortoise Ap♂ was recorded December 2, 1945 as having had injuries which left scars on scutes B and 1.

Tortoise aj♀ on February 1, 1941 was recorded as having injuries on plates D, 6, 7, 8, s, t and u, on which, a mass of irregular, newly regenerated horny material with a bone here and there hanging loosely in place was about ready to be displaced. An unbranded tortoise was found on April 9, 1942 which had a round scar on scutes C, D, 7 and 8 about 1¼ inches in diameter. Tortoise Cb♀ had a deep hole crushed in scute 8 on October 3, 1943.

Tortoise Do♀ has a peculiar history. She was first branded at Vertical Den on December 30, 1939. On her first recapture at the same place on February 20, 1943, it was noted that her shell had been so broken as to produce large cracks across the plastral edge of both bridges, both of which had then healed leaving the scar. Her empty shell with back removed and contents cleaned out by a predator was found a short distance southwest of Vertical Den on December 2, 1945.

SEX CHARACTERS AND RATIOS

Although the sexes are very much alike, there are four important characters which become progressively more divergent with age that help to differentiate between them. The gular projection, prong or "horn" is longer, larger and more upturned in the males, especially as they get older. The inguinal depression adapted to fit around the posterior portion of the female shell during copulation is also deeper and much more pronounced in older males.

The tail is longer, larger at the base and more conspicuous in the males in advanced age, but there is a good deal of overlapping in this character and young males are very difficult to distinguish from females by it alone. In maturity the males usually attain larger size than the females. See Table 2. By studying these four characters, adults can usually be distinguished with certainty and a large percentage of young tortoises can be placed satisfactorily, but even with careful study, there are a few that cannot be properly allocated.

This knowledge of sex characters has grown gradually. In the early part of the study, the sex was not always recorded because of uncertainty, but as one character after another became recognized, in-

creasing certainty tended toward more correct placement. Some tortoises were sexed only once, others several times. Some individuals were always recognized as males, others as females, but there was a doubtful group sometimes placed in one sex and sometimes in the other.

Of the 281 tortoises listed in our index, 101 are considered as males, 151 as females, 10 in the "sex indeterminate" group and the balance with sex unrecorded. Of the "sex indeterminate" group, 5 were most often recognized as males and 5 as females. Those listed as females, doubtless included some young males. The sex ratio cannot therefore be accurately determined from these data.

LIFE HISTORY

The life history of the Desert Tortoise is not well known. Some of it can be pieced together from the literature and some additions are made in this study. Hints of other aspects can be obtained from comparative information of other turtles or tortoises.

EGGS

The eggs have been well described. Miller (1932: 191) gives the following description, which agrees closely with our own observations. At time of laying, the egg is moist, translucent and extremely hard, with a coarse rough texture and irregular papillations and without any gloss, chalky layer or pigment. The translucence which permits observation of a small gas bubble disappears when the shell dries. Inside the shell is a very fluid albumen surrounding a thicker viscid layer enclosing the tough pale cream-colored yolk which it holds in position by means of a peduncle of this viscid albumen attached to the shell.

Eggs are nearly globular in general shape, but are more or less elliptical in both cross and longitudinal sections. Miller's measurements of diameters range from 41.6 x 36.7 x 34.9 mm. to 48.7 x 39.6 x 38.2 mm. He thinks the fact that the bubble remains for several months without enlargement indicates that the shell and albumen are moisture-proof.

EGG-LAYING

Observations of egg-laying are very inadequate. The evidence of Miller (1932) indicates that only one egg is laid at a time. He had a tortoise captured in the spring lay 5 eggs in captivity on a hard deck surface on October 4, 7, 8 and 30, 1916. He cited two examples of young tortoises hatching singly from "nests" in the desert. He also cited two observations by a student at Needles, California of a tortoise laying a single egg on June 17, 1923. In each case, the tortoise dug a hole 3 or 4 inches deep in sandy soil, with a hind leg, deposited one egg and used the same hind leg in covering it.

Grant (1936:227) reported that a tortoise laid 6 eggs at Victorville, California, June 9, 1935 and that in June, 1934, near Hodge, California, three females each laid 5 eggs and another female laid two eggs, all in holes dug by the hind feet. He says that it took an hour to dig a hole and fifteen minutes to lay the eggs. After an egg was laid, a foot was thrust into the hole, seemingly to roll or pack the eggs. When finished, the hole was filled and covered by the same process.

In our studies, a nest site was found in Big Den about 6 feet from the mouth, in which three eggs were probably deposited. It is not likely that the tortoise ordinarily deposits eggs singly in nature as suggested by Miller (1932). Hallinan (1923:11) shows that in the gopher tortoise egg sets range from 4 to 7 with an average of 5.

Cagle (1937:88) indicates that in the slider turtle, *Pseudemys troosti,* and others that the bladder and cloaca are distended with water to be used in softening the ground to assist in digging. Conant (1945: 41) described the nesting of a box turtle, in which the water from the bladder was released into the nest hole after it was dug and before the eggs were laid, explained on the theory of providing moisture for the eggs. Miller (1932) says that a considerable quantity of watery fluid was extruded with an egg so that the wet spot formed on the deck where the egg was laid was about 6 inches in diameter. Presumably the water from the bladder is used in egg-laying, even though Miller's student did not report it.

Miller's report (1932:190) that during egg laying on a hard surface, the posterior end was raised to the height of the hind legs while the front of the plastron touched the ground, may be explained on the theory that the tortoise normally has its hind leg in a hole during the process and in absence of a hole straightened the hind legs as in the normal position. Conant (1945:43) states: "I have watched perhaps a dozen other turtles of several species dig their nests, both in captivity and in the wild, and the process, basically, has always been the same."

Hallinan (1923) reports that the gopher tortoise deposits its eggs at the entrance to its burrow just inside the mound of dirt buried to a depth of 4 to 8 inches. He found 7 sets of eggs on May 28 and 2 sets on June 4 in such places. The regular place of deposit of eggs by the desert tortoise does not seem to have been fully elucidated.

During our field work, egg-shells indicating position of egg-laying have been encountered 8 times. On August 4, 1939, egg shells were found at the mouth of a summer hole. Similar egg shell fragments were excavated from the dirt in the bottom of winter dens near the mouth in Big Den and Twin A Den on October 7, 1939; in Twin A and Twin B dens on November 24, 1939; in East Den on December 30, 1939; and in Point Den on January 6, 1940. An additional site of egg-laying was found in Big Den about 6 feet inside the mouth on February 1, 1941.

These dates do not indicate time of egg-laying or hatching, but the records give positions of egg deposits. One of the records comes from a summer hole, the others from dens. These records suggest that probably the desert tortoise selects egg laying sites similar to those of the gopher tortoise at the mouth of burrows.

Grant's records include five sets all laid in the month of June and Miller gave another record of

eggs being laid in June. This is probably the usual time of egg-laying in nature despite the fact that there are several records of eggs being laid in captivity during the month of October.

INCUBATION

Development in the eggs of this tortoise has not been well studied. Baldwin (1940:50) speculated that embryonic excretions in a land tortoise would be stored in the allantois as uric acid. Grant (1936:228) mentioned opening an egg containing an embryo with a well developed blood system. In our studies, an egg containing a dead, but well developed young tortoise still in recognizable condition was, on February 1, 1941, dug out of a nest in Big Den from which it appeared that two others had hatched not later than the preceding fall.

The dried fetus from this egg shows the plastron and carapace well developed with identifiable sutures, but with no indications of growth rings. Each scute was covered with coarse papillations. A large yolk sac is attached to the center of the posterior part of the plastron, which is incomplete at that point and bulges outward to meet the yolk sac. There is a transverse suture indicated at the edges of the plastron but this is interrupted in the middle by the yolk sac. The neck is retracted within the shell and only part of the head projects from it. The egg tooth had not yet developed. The feet are flattened like aquatic flippers and armed with extra long needle-sharp claws that are closely appressed to one another. The fetus was so arranged that its longitudinal axis was parallel with that of the egg.

The transverse wrinkle across the plastron is probably an adaptation to fetal development in the egg. Miller (1932) thinks it is indicated by a more or less crumpled appearance of the plastron which takes some months to smooth out. He says the nuchal and caudal plates are both incomplete at hatching. This is also true of the gular and anal plates of the plastron. Grant (1936:228) says the young tortoise in the egg lies partly curled and at right angles to the long axis of the egg. This must be a later stage in fetal development than that of the fetus of the preceding description.

Grant (1936:227) reported numerous cases where eggs hatched about mid-August; other cases where eggs hatched September 2 and 15 and a case of a captive tortoise laying 6 eggs on June 9, 1935, of which one hatched, 4 were unhatched and one was infertile on October 7, 120 days later. He also reported a case of another captive tortoise laying 5 eggs in June, 1934, of which 4 hatched in November and one the following March, 5 and 9 months later respectively. Why eggs of the same brood develop at such different rates has not been explained. Miller (1932:192) reported finding two hatchlings about mid-October, which tends to corroborate the idea developed from other evidence that the peak of egg laying occurs in June and the peak of hatching in September or October.

Whether there is much delayed spring hatching in this tortoise such as the one egg reported by Grant (1936) is not known. Hartweg (1944:20) has shown it to be a common practice in the Painted Turtle. The process of hatching in this tortoise does not seem to have been described. Chace (1945:420) has reported and photographed the process in the Snapping Turtle.

HATCHLINGS

Grant (1936:228) described a young tortoise that hatched on October 7, 1935 as having an egg tooth on the end of the snout, with which, it cut its way out of the egg; also a yolk sac in the middle of the abdomen and a clear thick jelly-like substance under the plastron. The jelly soon became dry, but the yolk sac was not fully absorbed until the second day. Miller (1932:194) says that the umbilical area is quite incomplete at hatching and the distortion at the umbilicus persists for more than a year.

A hatchling in the possession of the senior author about 1928 (Fig. 9) had not only a distorted umbilical area and a portion of the yolk sac in evidence, but also several small wrinkles surrounding the umbilicus and a large one crossing the plastron from bridge to bridge. The figure also shows a dorsal view of the scutes before any growth rings have appeared. Van Denburgh (1922:988, pl. 125) shows a cut of a small tortoise (Fig. 10) with one growth ring on the scutes in which the wrinkles around the umbilicus have smoothed out, but the one across the plastron from bridge to bridge has not quite disappeared (May, 1912). The umbilicus has changed considerably and the remnant of the yolk sac appears to be gone.

Grant (1936) thinks the egg tooth is not shed, but flattens out after several months. Miller (1932) thinks it disappears during the second year. The claws are needle sharp at hatching and remain so until dulled by use. Claws are maintained throughout life in approximately balanced proportions between front and hind limbs, the front limbs being used later for digging burrows and the hind limbs, at least in the female, for digging nests for the eggs.

The shell is soft and pliable at hatching and ossification is very slow in hardening it. Miller (1932) says the shells of young tortoises kept in captivity three years were still soft and still larger ones with soft shells had been picked up on the range. Grant (1936) thinks that the shell is hard enough to resist carnivores when about 100 mm. in length at five years of age. The ossification process does not seem to have been studied histologically.

The position of the fetus in the egg not only explains the crumpling of the plastron, but also the peculiar proportions of the hatchling. Grant's measurements of one hatchling show that it was actually wider than it was long and that this proportion rapidly changed after emergence. His figures are quoted, the first in each case being length in mm. and the second width: 36 x 39 on October 7, 41 x 37.5 on October 8, 44 x 36.5 on October 11, 1935; 44.5 x 36.5 on June 18 and 48 x 42.5 on August 15, 1936. These give width-length ratios of 1.085, .915, .831, .821, and .886, respectively.

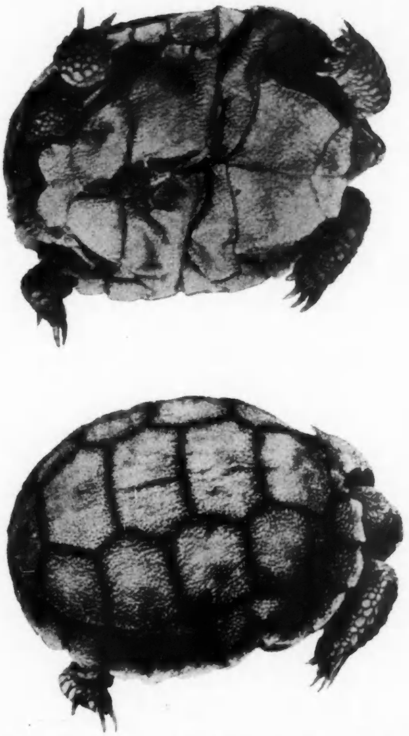


FIG. 9. Hatchling tortoise showing distorted umbilical area, transverse suture and lack of growth rings on scutes. From Woodbury's Reptiles of Utah.

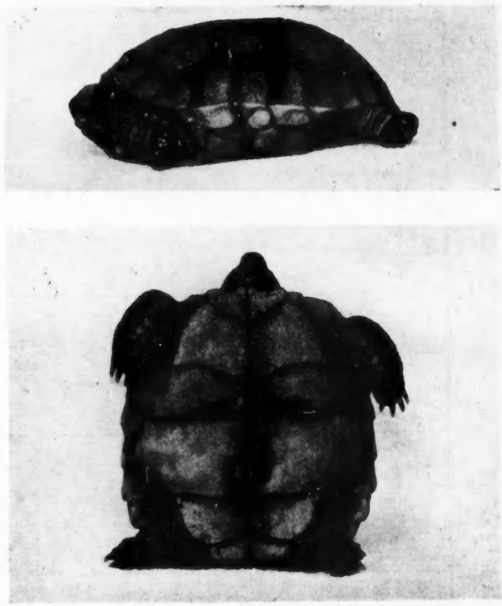


FIG. 10. Hatchling tortoise showing advancement of development beyond that shown in Fig. 9. Courtesy of Calif. Acad. of Science.

The scutes on the carapace of newly hatched tortoises vary in color from dull mustard yellow to warm light brown (Miller, 1932) with darker edgings along the sutures and in irregular blotches on the scutes. The plastron is slightly lighter. They are usually covered with a peculiar bloom which Miller thinks may be dried albumen and which is gradually lost.

Grant (1936) reports that very young tortoises exhibit marked pugnacity, bucking forward with open jaws with head at a 45° angle and hissing if touched on the carapace.

DEVELOPMENT OF THE YOUNG

In our studies, very few young tortoises have been found among the population. Field notes show that one very small tortoise was found on the flat west of Big Den on May 6, 1939; that two dead "dollar size" tortoises were found in Cove Den on November 30, 1940; the remains of a tortoise, bearing 4 growth rings on each scute had been partly eaten by a predator when found on the area April 12, 1941; a dead tortoise about 73 mm. in length and having about 10 growth rings was found April 11, 1942; a live tortoise of 88 mm. length was found in the shade at the mouth of Trash Den on June 1, 1941; a dead tortoise with a hard shell about 150 mm. in length partly eaten by a predator was located on the area on April 12, 1941.

All of the foregoing up to the 88 mm. length had more or less soft shells, i.e. the bones underlying the scutes were pliable, although there seems to have been a gradually increasing rigidity in the larger sizes. Somewhere between the 88 and 150 mm. size, the flexibility seems to have been reduced to a negligible quantity.

Miller (1932:198) gave measurements of 10 young tortoises taken over periods of one to three years, in which it appears that 5 hatchling or very young tortoises gained an average of 3.1 mm. in length during the first year, but another small one (46.9 mm.) gained 23.5 mm. in the same time. Three of five small ones gained an average of 4.7 mm. during the second year. One of the five gained 16 mm. in the third year.

Two other young tortoises of 85.2 and 93.3 mm. showed gains of 7 and 8.1 mm. in one year and 6.1 and 5.2 mm. in the second year. The ninth tortoise grew from 106 to 110.5 mm. in two years and the tenth from 123 to 130 mm. in three years. His tortoise of length 72.3 mm. at age 3 years was still soft shelled, but one he found of length 85.2 mm. was firm and he estimated that firmness was acquired at length 80 mm., approximately four or five years of age. Grant (1936:228) estimated that the change occurs by the time they are 5 years of age and 100 mm. in length, which agrees more closely with our data.

A 5½-year-old tortoise of 98 mm. length with a

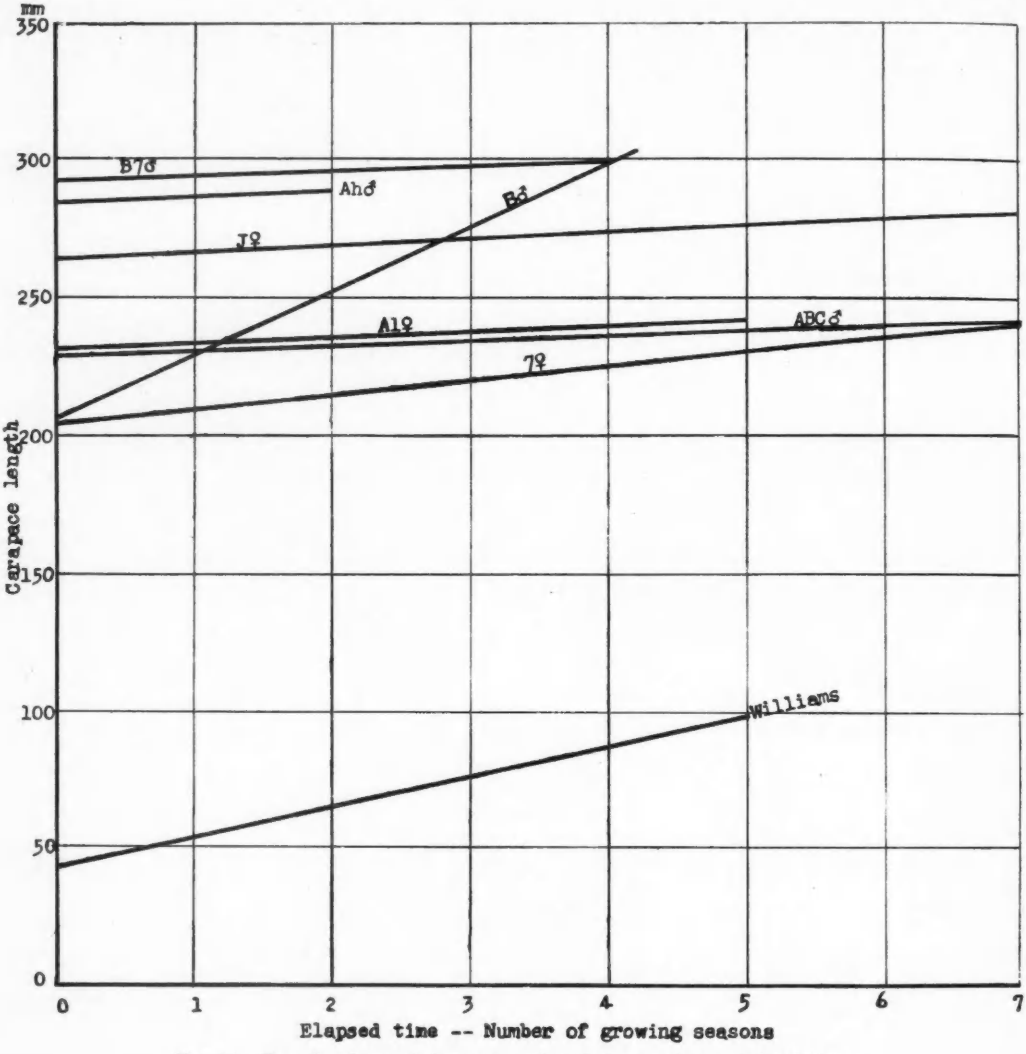


FIG. 11. Records of growth in carapace length for varying periods of time.

pliable shell brought to the University by Mr. and Mrs. Marshall C. Williams of Salt Lake City on April 13, 1946 had been captured by them about 5 miles southeast of Indio, California on November 1, 1940 when it was a hatchling. In captivity, it had fed principally upon lettuce and had grown rapidly for the first three years but showed little gain in size during the last two years when left to the care of others (Fig. 11). The scutes bear six growth rings.

The rings on the scutes are doubtless correlated with growth, but the causes, rate and nature of the correlation are obscure. It is easily demonstrated that there are increasing numbers of rings with increasing age and size. Successive size and shape of scutes are indicated by successive rings. Careful scrutiny of a scute in which the hatchling scute is still in place reveals that each successive ring appears to be the edge or extension of a slightly larger horny plate that has grown underneath its predecessor.

It is this projection arond the edge that makes the ring. Such rings are not uniform. Some are wider than others. Some are incomplete. Individual rings are not uniform, being wider in some places than others. Such irregularities are produced by greater growth in one area than in another and allow for expansion where needed in growth with consequent change in form or proportions of the tortoise.

Whether each ring represents the edge of a complete plate that underlies the one above or whether it is merely an extension under the edge has not been determined. Miller (1932:195) seems to regard it as

the latter. He shows that age cannot be computed from the rings, which agrees with our conclusions. It is highly probable that the growth of the scutes keeps pace with some fundamental growth underneath, probably that of the bone of the shell.

ADULTS

Beyond the 100 mm. stage, after the shell is hardened, growth continues in a more or less similar fashion until a size is reached where growth is much retarded or entirely stops. The adult, thereafter, appears to remain approximately constant, perhaps with small variations of contraction and expansion. The ultimate adult size varies in different individuals and probably also in different sexes (Figs. 11, 12). It seems probable that rate of growth is relatively rapid in the young and gradually slows down to a stop at maturity.

Interpretations from our tabulations (Table 2), indicate that adult length varies from about 230 to 265 mm. in females and from about 250 to 300 mm. in males with possible extremes slightly beyond these figures. The greatest growth recorded in our studies is that of B♂ from 206 mm. in length November 5, 1938 to 302 mm. on March 19, 1943, something less than 100 mm. in 4⅓ years or an average of 24 mm. per growing season. The greatest growth recorded in a female is that of 7♀ from 204 mm. on November 5, 1938 to 239 mm. on November 4, 1945, which amounts to 35 mm. in 7 years or an average of 5 mm. per season.

Some other tortoises which showed growth, but at a less spectacular rate include: ABC♂ from 229 mm. on November 5, 1938 to 242 mm. on January 19, 1946 or 13 mm. in 7⅙ years, an average of 1.8 mm. per growing season; E♂ from 263 mm. on May 15, 1943 to 269 mm. on November 17, 1945 or 6 mm. in 2½ years, an average of 1.8 mm. per growing season; j♀ from 267 mm. on November 5, 1938 to 281 mm. on November 17, 1945 or 14 mm. in 7 years, an average of 2.0 mm. per growing season; al♀ from 232 mm. on February 18, 1939 to 242 mm. on February 20, 1944 or 11 mm. in 5 years, an average of 2.2 mm. per growing season. The average growth rate per year for these five fastest growing males is thus 6.5 mm. in length per growing season and for the two fastest growing females is 3.6 mm. in length per growing season, or an average of 5.7 mm. for the seven tortoises.

Published measurements of the gopher tortoise (Goin & Goff 1941:66) showed that 33 tortoises increased an average of 11.5 mm. in length and 6.1 mm. in width in approximately one year. Only one failed to increase in size. Could it be possible that they were working with a younger population from which most of the older tortoises had been removed by human interference in much the same way as the adult population of the desert tortoise is now being depleted?

There are in our records the measurements of 50 tortoises that have been measured from 2 to 6 times over periods ranging from one to seven years which show no appreciable change in size (Table 2). This is a clear indication that an adult stage is reached in which little or no further growth occurs. As tortoises get older, the scutes tend to become worn and many of the earlier rings disappear.

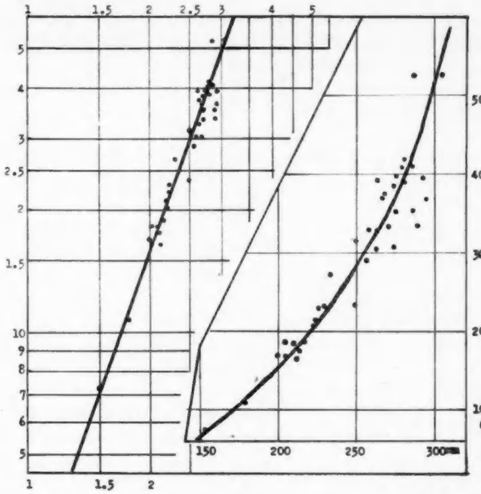


FIG. 12. Graphs showing weight of tortoises plotted against length. Left, on double logarithmic paper showing straight line. Right, or linear graph paper showing curve.

How long the adult stage lasts is unknown and no method has yet been devised by which it can be accurately predicted. However, our recapture records throw light upon the problem. Of the original 12 adult tortoises painted on November 28, 1936, six of them were recaptured as late as 1945, about 9 years later; 2 others as late as 1944; 3 others as late as 1941 and one in 1939.

These 6 records of tortoise recaptures over a period of 9 years of adult life prove only that 9 years is a fraction of the adult life span, but do not indicate the size of the fraction. Available evidence leads us to believe that it is not a large fraction. The tortoise doubtless has a long life.

The age at which sexual maturity arrives is not known but a rough calculation can be made. If tortoises reach the 100 mm. length in 5 years (Grant 1936:228), the average rate of growth would be about 12 mm. per year. At the same rate of growth, maturity would probably be reached in 10 to 15 additional years. Upon this basis, then it might be estimated that maturity would be reached somewhere between 15 and 20 years. While this cannot be considered accurate, yet it gives an hypothetical thinking scheme which can be corrected as recapture records and measurements accumulate. The final solution may require the application of additional techniques.

COURTSHIP AND MATING

Grant (1936:227) quoted Robert Heckly to the effect that his captive tortoises that were brought out of hibernation began mating in March and finished

by the last of April. He also stated that males utter grunting sounds while courting. This does not agree with Miller (1932:197) who states that in captivity courtship extends over most of the warmer parts of the year.

When tortoises meet one another, they generally approach with necks outstretched and heads bobbing up and down until their noses almost meet. Sometimes only one tortoise makes such an advance and is not reciprocated. If one is a female, a courtship may follow. Miller says the female may retract or go on feeding or dozing in the sun, in which case, the male circles about, nipping clumsily at the edges of the female's shell, or if she remains retracted, the male may lunge at her with his gular "horn" but not with the same pugnacity used against another male.

Camp (1916:515) reported that "the males court their mates by biting them gently around the edges of the shell. During copulation the male stamps his hind feet and utters a mechanical grunt with the head hooked over the plastron and the mouth half open."

Miller (1932:107) states that mating activity has been observed again and again in captivity, but no actual intromission could be detected, and eggs deposited in captivity were not fertile. It was his impression that animals needed loose ground and not a hard floor to complete coition.

In the laboratory at the University of Utah on April 16, 1946, a large male tortoise, a small male and a small female had just been fed fresh alfalfa. The small female had started to eat when the large male moved toward her with neck outstretched in a lateral curve and tried to nip her on the head and front legs. The female turned away, the male following and round and round they went in a circle four or five times. Then the male stopped, put his front feet on her back and tried to mount, got part way up but slipped down.

While resting, he spied the small male who was eating and began biting at head and legs. This started a series of circles (about 3) and then the large male tried to mount the small one, having better luck than in the previous case, getting almost into position with his inguinal depression against the other one's pygal plate. Then started a series of movements in which the tail was thrust far forward through his anal notch toward the cloaca of the other; the hind legs were pulled up off the floor allowing the pygal plate to strike the floor with a slight clicking sound. This was repeated several times but there was no cooperation from the other individual and no intromission could be observed. He soon lost interest and left.

An attempted coition was observed by the junior author at St. George on a cement floor in Dixie Junior College. Three tortoises had been captured on the Beaver Dam Wash on April 5, 1941 and brought back to the college. On April 8, about 9:30 a.m. a male tortoise was observed biting the anterior edge of the carapace of another male although a small passive female was also present. The aggressive male continued his activity biting and also pushing the other one around for about ten minutes.

Later in the day, about 3:15 p.m., the aggressive male resumed activities. When observed, he was standing upright behind the other male, with the inguinal depression of his plastron fitted against the caudal plate of the carapace of the other tortoise. He held himself upright by dropping his front feet on to the posterior part of the carapace below and stretching head and neck forward to maintain balance.

The tortoise being ridden seemed uninterested and unconcerned as it crawled about, but the other followed in the erect position wherever it went. The forward movement, however, was complicated by a vertical up and down bobbing motion which produced a clicking sound as the pygal scute hit the cement floor.

The aggressive male was obviously attempting to copulate. He was observed from time to time to push the tail forward to make contact, but no actual intromission could be seen. About this time, a puddle of liquid containing white and gray solids, probably from the urinary bladder, was released on the floor. About a minute later another similar puddle appeared.

Within another 2 or 3 minutes, the movements upset his balance and he had to drop down on the floor. However, he quickly remounted on the left side and again began bobbing up and down and thereafter spilled a larger puddle of liquid. This was suddenly terminated when the lower tortoise moved and he fell off.

While we have not actually witnessed the mating activity in the field, yet the junior author encountered a pair of tortoises on the flat about ¼ mile NE of Telwire Den in late afternoon on July 15, 1940 that had probably just completed the act. When approached, the female ran to a nearby summer hole. Both members of the pair 1h♂ and BF♀ had wet mud around the cloaca of each and there was a muddy spot on the ground nearby. At this place, the dirt on an area about 18 inches in diameter had been treaded by the feet of tortoises until all the rocks had been pushed out of the way and the dirt was fine and dusty except where the wet spot had made it muddy.

SOCIAL BEHAVIOR

On the second visit to the dens on November 25, 1937, several tortoises were taken out of dens and left sitting in the sun in a semi-dormant condition. When tortoise Cj♂ got warmed up to 85° F. (29.5° C.), he became active and approached another tortoise that was still inactive. He attempted to bite the front leg of the other, and then lunged forward and bumped the other with his gular "horn." This was repeated many times, on some occasions with such force as to move the passive tortoise 2 or 3 inches.

On another visit nearly a year later on October 28, 1938, a group of 13 tortoises taken from the dens was left sitting in the sun. After temperatures reached the activity level, they became so active that it was difficult to hold them together and different types of behavior became manifest. In one case, like

the preceding, an attacking opponent became so vigorous that the recipient was jolted out of passivity. At one time the attacker hooked the gular process in the anterior opening of the shell and with one or both front feet over the carapace, he proceeded to toss or wrestle the other around in vigorous and grotesque fashion for several minutes before satisfying his pugnacity (Fig. 13).

Other tortoises showed the mutual approach system in which two tortoises approached each other with necks outstretched and heads bobbing, sometimes repeating at frequent intervals, sometimes turning attention to other individuals. In the melee some became pugnacious and lunged with the gular process at various other individuals. In one or two cases, mutual bouts developed.

In still other cases, after mutual nodding acquaintance, two tortoises turned and started off together. In one or two cases, it was suspected that the procedure took on an air of courtship behavior, but no approach to mating was observed. The whole affair, however, indicated the presence in the tortoises of instinctive behavior patterns based upon social attractions that betoken the existence of a feebly social aggregation. It has been shown (p. 168) that the concentrations of tortoises in dens is in part due to feeble social attractions.

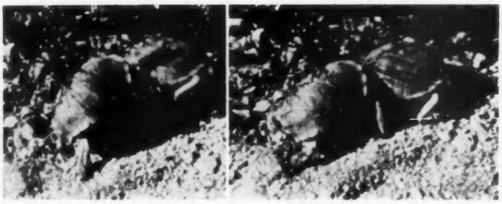


FIG. 13. View of pugnacious tortoise attacking another.

ECOLOGY

ECOLOGICAL BACKGROUND

CLIMATE

The climate of the area can be estimated in a general way from United States Weather Bureau records, even though there are no stations located close to the study area. The records most applicable are those from stations at St. George, Leeds, Springdale, and Hurricane in Utah and at Logandale, Nevada, which are summarized in Table 3 abstracted from United States Department of Agriculture Yearbook, 1941.

It is obvious from this tabulation that the general characteristics of the climate include great variations in temperature, long growing season, and sparse precipitation; but in addition it should be noted that there is little cloudiness, low humidity, great intensity of sunshine, and infrequent snowfall.

These great variations in temperature involve an average daily fluctuation of 35 to 40° F. and an average seasonal fluctuation between January and July of 43.5° F. but extreme annual maximum and minimum temperatures often differ more than 100° F.

TABLE 3. Climate at five stations in Utah and Nevada.

		TEMPERATURE					KILLING FROST				PRECIPITATION	
	Altitude	Length of Record	January Average	July Average	Maximum	Minimum	Length of Record	Last in Spring	First in Fall	Growing Season	Length of Record	Annual
NEVADA												
Logandale	1700	33	44.6	87.3	120	6	33	Mar 19	Nov 11	237	33	5.31
UTAH												
St. George	2800	39	38.4	82.9	116	−11	38	Apr 10	Oct 23	196	40	8.73
Leeds	3400	24	35.7	80.3	115	−15	24	Apr 10	Nov 5	209	27	12.71
Springdale	3981	32	39.2	81.4	112	−15	29	Apr 15	Oct 28	196	32	14.51
Hurricane	3250										17	11.05
Average		32	39.5	83.0	115.8	--8.8				209.5		10.46

	PRECIPITATION												
	January	February	March	April	May	June	July	August	September	October	November	December	Annual
Logandale	.79	.69	.49	.29	.14	.14	.46	.58	.30	.48	.37	.58	5.31
St. George	.93	1.11	.88	.54	.39	.22	.88	.95	.64	.78	.57	.84	8.73
Leeds(near)	1.73	1.93	1.32	1.05	.65	.31	.73	.92	.59	1.03	.77	1.68	12.71
Hurricane	1.15	1.33	1.03	1.04	.67	.38	.78	1.00	.83	1.27	.62	.95	11.05
Springdale	1.49	1.75	1.69	1.17	.79	.26	1.12	1.59	1.23	1.07	.99	1.36	14.51
Average	1.22	1.36	1.08	.82	.53	.26	.79	1.01	.72	.82	.66	1.08	10.46

and have been recorded as differing by 127° F. It is seldom that temperatures go below 0° F. in winter but it is not unusual for them to exceed 100° F. in summer.

The so-called growing season which ranges at these stations from 196 to 237 days is based upon the frost-free period but this seldom marks the limits of growth of native plants. Many plants are limited in growth by soil moisture as well as temperature. This is especially true of annuals but is in lesser degree applicable to many of the perennials.

It may be noted that the table showing monthly precipitation indicates a double cycle with low points in June and November. These drouth periods are characteristic but not necessarily constant as previously indicated by Woodbury (1933:156), where he referred to "a double cycle of alternating wet and dry periods, the wet periods occurring (1) in winter and early spring, and (2) in late summer; the dry periods occurring (1) in late spring and early summer, and (2) late in the fall."

> These figures, however, give but slight idea of the actual conditions, for in general, the annual cycle does not tend to follow the mean. . . . The mean is no definite indication of what is bound to occur, and is ordinarily not the critical period of tolerance or the limiting factor in the distribution of organisms. The critical period is the extreme which often goes much beyond the limits indicated by the means.

Another characteristic of the desert climate is the tendency at night for cold air to drain down the canyons into the lowlands and lift the warmer air to

the foothills (Alter 1941:1157). This tendency is upset by wind which usually wipes out the differential.

This is illustrated in the records made at two stations at St. George, Utah, for the month of February, 1946. The records of the U. S. Weather Bureau station located in the bottom of the valley at 2800 feet altitude yield minima varying from 17° to 33° F. (−8.3 to .6° C.) with an average of 25.9° F. (−3.4° C.) whereas those at the municipal airport located on the exposed flat top of a volcanic ridge southwest of the city at 3050 feet altitude yield minima varying from 20 to 39° F. (−7.6 to 3.9° C.) with an average of 30.3° F. (−.9° C.). These minima of the hilltop are usually a few degrees higher than those of the valley, varying in this case from −1° to 8° F. difference. The difference in the maxima are usually reversed, the temperatures of the valley generally being higher than those of the hilltop.

In order to relate the weather records at St. George to those of the study area, thermographs were set at St. George Municipal Airport at 3050 feet and at East Den on Beaver Dam Slope at 3300 feet so as to run simultaneously for the six days from February 4 to 9, 1946 inclusive, both being set as nearly as possible under similar conditions of slope and exposure. Despite the 250 feet higher altitude, the record on the Beaver Dam Slope showed both the maxima and minima to be greater by an average of 4.2° F. in each case than the record at St. George. Could this be due to its foothill location at the west base of the Beaver Dam Mountains?

Soil Characteristics

The topsoil is a buffy-colored fine sandy loam. The next horizon, after removal of particles larger than ½ inch in diameter, can be classified as a fine gravelly loam slightly lighter in color than the surface material. Particles of angular-shaped gravel project above the baked surface of the soil. These gravels vary in color from white, brown and dark gray to black. Large boulders are exposed here and there, but these are more numerous in the bottoms of the four- to twelve-foot deep washes which transverse the area. The soil varies in depth from a few inches to about three feet. Beneath this there is a layer of fine limestone gravel, with frequently a thin hardpan above it. This limestone gravel is loosely bound together and is somewhat porous because of the lack of fine particles in the interstices. Digging in this layer below the hardpan, while slow and difficult, can be accomplished with a sharp-pointed shovel.

The soil from lower horizons is coarser than is the top soil. This can be illustrated by the sifting of a sample of soil from the area. The terms of soil nomenclature used here are those proposed by Hardy (1945:77). A sample of topsoil contained 23.4% by weight particles coarser than ½ inch in diameter. The remaining material sifted had the following composition: Granule gravel, 19.8% Coarse sand, 10.0%; Fine sand, 21.6% and Silt and Clay, 48.6%. At one foot in depth, after removal of particles coarser than ½ inch in diameter, the percentages were: 35.7%, 7.9%, 15.3% and 41.1% respectively. At a depth of two feet; 49.3%, 26.0%, 15.8%, and 8.9%.

The soluble carbonates in the soil samples analyzed varied from 0.01 to 0.02% while the total carbonates present as shown by the evolution of carbon dioxide by 1.4 normal hydrochloric acid is very high. Because of the presence of magnesium carbonate and similar heavy carbonates, the concentration is expressed as percentage of carbon dioxide released by the acid. In the topsoil, this was 17.5% while it was 19.5% at one foot depth. At two feet in depth this was 45.1%.

At two feet in depth, the sodium chloride present was 0.05% and the sodium sulphate 0.06% but neither one was found in the upper horizons. These soluble sulphates and chlorides which have been leached out of the upper layers are present in the deeper gravels where they occasionally form white lines of crystals on exposed banks.

The texture and composition of soil is of vital importance to tortoises because they spend so much time underground where protection is afforded from summer sunshine and winter cold. They are more or less limited to areas where underground protection can be obtained. Few areas in this region furnish any natural cavities where such protection is available and it devolves upon the tortoises to improvise their own shelters.

They dig their own holes. Obviously, best results would be achieved where soil is sufficiently free from rocks to permit digging and where it is compact enough to maintain an archway over the hole after it is dug. Soil type therefore becomes a critical factor in tortoise distribution within their range, more or less restricting them to suitable soil types.

Plants

Plant names, unless otherwise indicated, are those given by Tidestrom 1925, hence authors are not quoted. The upper slopes of the Beaver Dam Mountains bear typical open stands of the pigmy conifers of junipers and pinyon pines, which reach downward to about 4000 or even to 3700 feet in altitude. Overlapping the lower portions of the pigmy conifers is an inconspicuous stand of the small black brush, *Coleogyne ramosissima,* which grows among the conifers and extends down the lower slopes of the mountains and into the foothills, but tends to give way on the gentle desert slopes to an open stand of the top-heavy tree yuccas or Joshua trees, *Clistoyucca brevifolia,* which overshadow the lowly black brush. This Joshua tree stand is in turn overlapped by the less conspicuous broad-leaved evergreen shrub, the creosote bush, *Larrea tridentata,* which extends downward onto the lowest slopes, benches and valleys.

The area studied lies in the Mohavian Biotic Province of Dice (1943:54) or the Lower Sonoran Life Zone of Merriam which is characterized by creosote bush, *Larrea tridentata,* and its associates (Tidestrom 1925:9). Clements (1920:170) lists it as the Western Desert Scrub Association, while this area has been described as the Clistoyucca-Larrea Association by Hardy (1945:37).

The widely-spaced evergreen Joshua trees (Fig. 1) varying from 6 to 15 feet in height, average approximately 48 per acre and occupy about 2½% of the area. The largest shrubs, creosote bushes, conspicuous because of their persistent dark green foliage and dark stems, number about 218 per acre and occupy about 5% of the area. The spiny red-berried *Lycium andersonii*, and the Mormon tea, *Ephedra nevadensis*, have about the same number of plants, but occupy respectively about 3% and 2% of the area. The burro bush, *Franseria dumosa*, with pale gray foliage and small rounded shape is most numerous, there being about 823 per acre, covering about 4% of the area. Winterfat, *Eurotia lanata*, with its silvery-gray foliage is found in scattered areas. As estimated from a 60 by 60 foot quadrat, in an average patch, the winterfat plants numbered about 545 per acre and covered about 1% of the area.

These most numerous large and conspicuous plants occupy approximately 17½% of the surface. Some of the intervening space is occupied by other perennial shrubs and cactuses but much of the ground is bare and exposed to the sun except when blanketed with numerous small annuals at certain seasons of the year.

These other perennial shrubs, moderate in number, include *Krameria glandulosa; Salazaria mexicana;* oil bush, *Thamnosma montana; Ephedra torreyana; Encelia frutescens virginensis;* paper flower, *Psilostrophe cooperi;* purple sage, *Salvia carnosa; Tetradymia axillaris; Hymenoclea salsola;* and matchweed, *Gutierrezia lucida.*

Colonies of the spreading daggerlike *Yucca baccata* are irregularly distributed over the area. The arborescent cactus, *Opuntia echinocarpa*, and a number of types of prickly pear, *Opuntia* sp., and of Echinocereus also occur.

In the early springtime, a cover of annuals fills the interspaces. The abundance of the several kinds and the period at which they occur varies somewhat from year to year depending upon the temperature and the amount of rainfall of the preceding period. Some of these abundant annuals are the dwarf milkvetch, *Astragalus nuttallianus trichocarpus;* cheat grass, *Bromus rubens;* desert plantain, *Plantago scariosa;* and alfilaria, *Erodium cicutarium.* Less abundant are *Welwitschia floccosa, Eriogonum inflatum, Eriogonum deflexum, Gilia leptomeria, Ptiloria exigua, Calochortus flexuosus,* and *Delphinium amabile.*

Grasses most common, next to the ever-present annual cheatgrass, are the scattered clumps of galleta, *Hilaria rigida;* fluff grass, *Triodea pulchella;* and the common mesquite grass, *Muhlenbergia porteri*, which grows up through the shrubs of the area. Indian rice grass, *Oryzopsis hymenoides*, is common in certain small areas.

Along the temporary watercourses in the bottoms of the gravelly washes are found numerous large (4 to 5 feet high and 6 to 10 feet in diameter) rounded, dark-green bushes of the deciduous-leaved desert almond, *Emplectocladus fasciculatus.* There is also a greater number of *Salazaria mexicana* shrubs than on the intervening flats. The climbing milkweed, *Funastrum heterophyllum*, is occasionally found in the few small sandy areas of these washes, but the other plant life is much the same as that of the adjacent range.

ANIMALS

Each spring, herds of sheep pass over the area. They frequently denude the annual plant cover by grazing and trampling. Often almost the only annuals and grasses remaining are those which grow about the base of and up through the perennial shrubs and cactuses. The degree of denudation varies somewhat from year to year. Sometimes when the snow has receded and temperatures are high enough in the mountains, the sheep leave the area before the spring rains, and some annual growth develops after they are gone. In the winter, cattle graze over the area and browse on the winter vegetation.

Among the native mammals, carnivorous forms which could likely destroy either young or old tortoises are the desert bobcat, *Lynx rufus baileyi;* desert coyote, *Canis latrans estor;* desert kit fox, *Vulpes macrotis arsipus;* gray fox, *Urocyon cinereoargenteus scotti;* badger, *Taxidea taxus taxus;* spotted skunk, *Spilogale gracilis saxatilis;* and the Nevada ringtail, *Bassariscus astutus nevadensis.*

Rodents, which help loosen the soil and provide softer areas for digging often favored by the tortoises, include the antelope ground-squirrel, *Ammospermophilus leucurus leucurus;* the kangaroo-rats, *Dipodomys merriami merriami* and *D. microps woodburyi;* Mohave pocket-mouse, *Perognathus formosus mohavensis;* the scorpion-mouse, *Onychomys torridus longicaudus;* the cactus mouse, *Peromyscus eremicus eremicus;* and the canyon mouse, *Peromyscus crinitus stephensi.* The desert pack-rat, *Neotoma lepida lepida*, builds its nest-concealing litter piles in brush and in tortoise dens. At the south end of the area, a few workings of the pocket-gopher, *Thomomys bottae virgineus*, have been observed.

Of the rabbits, the Arizona cottontail, *Sylvilagus audubonii arizonae;* and the desert jackrabbit, *Lepus californicus deserticola*, vary in abundance from year to year. Some observations regarding mammals of the area have been reported separately (Hardy 1945:95).

Birds of the region have been reported by Hardy & Higgins (1940:95) and by Behle (1943:5). Typical nesting residents include the Gambel quail, *Lophortyx gambelii gambelii;* the Yuma ladder-backed woodpecker, *Dryobates scalaris yumanensis;* northern cactus wren, *Campylorhynchus brunneicapillus couesi;* western mockingbird, *Mimus polyglottos leucopterus;* Nevada shrike, *Lanius ludovicianus nevadensis;* Scott oriole, *Icterus parisorum;* and the desert sparrow, *Amphispiza bilineata deserticola.* These birds likely have little if any direct effect upon the tortoises other than the usual one of helping to keep down insect plagues so that plant life may thrive.

Of more direct importance to the tortoises would be the prescnce of such birds of prey as the western red-tailed hawk, *Buteo jamaicensis calurus;* the golden eagle, *Aquila chrysaetos canadensis;* the

prairie falcon, *Falco mexicanus*, the eastern sparrow hawk, *Falco sparverius sparverius;* and the western horned owl, *Bubo virginianus pallescens.* The western burrowing owl, *Speotyto cunicularia hypugaea,* is scarce, but one is believed to have nested in Rex Den during the spring of 1941 and again in 1942.

Reptiles, other than the tortoise, which have been taken in the area include the following lizards: the banded gecko, *Coleonyx variegatus utahensis;* collared lizard, *Crotaphytus collaris baileyi;* leopard lizard, *Crotaphytus wislizenii;* chuckwalla, *Sauromalus obesus obesus;* gridiron-tailed lizard, *Callisaurus draconoides gabbii;* desert scaly lizard, *Sceloporus magister magister;* brown-shouldered lizard, *Uta stansburiana stejnegeri;* desert horned lizard, *Phrynosoma platyrhinos platyrhinos;* and the desert whiptail, *Cnemidophorus tessellatus tessellatus.* Two of these commonly hibernate in tortoise winter dens.

Snakes taken in the area include: the red racer, *Masticophis flagellum frenatus* (piceus?); desert gopher snake, *Pituophis catenifer deserticola;* spotted night snake, *Hypsiglena ochrorhyncha deserticola;* sidewinder rattlesnake, *Crotalus cerastes cerastes;* Great Basin rattlesnake, *Crotalus viridis lutosus;* and the Mohave rattlesnake, *Crotalus scutulatus scutulatus.* All but the last-named species are known to enter tortoise dens, many of them for hibernation purposes. Other reptiles of the general area which may occur are recorded by Woodbury (1931:18).

The invertebrates of the area have not been studied in detail.

ADAPTATIONS

An adaptation may be regarded as an hereditary morphological structure, a physiological function, or a behavior pattern which enables its possessor to meet the exigencies of its environment efficiently. An adjustment is a change of structure, function or behavior within the limits set by its hereditary adaptation made to meet minor variations or fluctuations within the range of conditions in its habitat.

Adaptations of the desert tortoise to fit the desert environment are many and varied. They center mainly around temperature, water, food and predator problems and involve structure, function and behavior in complex ways.

Passive Resistance

The most conspicuous adaptation is the passive resistance to predators, in which the head is completely retracted and the legs are folded into the openings of the heavy shell and the short tail is twisted to one side. This is correlated with a muscle tension which holds the legs and tail rigidly in position.

Initiation of such a pattern varies considerably with the conditions. If the tortoise is active and is stimulated to resort to the pattern by sight of a recognized enemy, the action is more or less explosive, in which the tortoise drops suddenly to the ground, withdraws its head so quickly that air in its lungs is forced out the nostrils rapidly enough to make a hissing sound, and the legs and tail are brought firmly into position.

The behavior pattern is less spectacular if the action is triggered when the tortoise is at rest with the head already partly withdrawn and the legs loosely held in the openings of the shell. The action then consists mainly in finishing the withdrawal of the head which does not usually produce a hissing sound, and tightening the legs in the edge of the shell. Camp (1916:513) describes the hissing sound when disturbed in burrows and it has been observed occasionally during these studies.

During hibernation, the action is still less spectacular, sometimes scarcely noticeable. The head is often almost completely retracted and the legs already almost in position when at rest in the den in winter. If disturbed by a touch, there is usually a slow tensing of the legs to finish the passive resistance pattern although occasionally it is more explosive and the hissing sound is sometimes produced.

Active Resistance

During the process of removing tortoises from dens, it was noted that when disturbed, some of the tortoises moved farther into the den. When pulled backward by the hook, some tortoises retained the passive resistance pattern until removed, but others reversed the behavior pattern and gave active resistance by lowering the legs to the ground and attempting to move forward. In so doing, the shell was raised off the ground and in the low tunnels this often resulted in pushing the carapace of the shell against the top of the tunnel and effectively blocking the removal. Often, the hook was displaced by the action and the tortoise then moved forward, attempting to get out of range. Camp (1916:513) reported a similar behavior in burrows in southern California.

Recovery from Upside-down Position

Closely associated with this behavior is a positive pattern of recovery when turned over on its back. This behavior has been partly described by Camp (1916:515), by Jaeger (1922:257), by Pope (1939:240) and by Cassell (1945:25). Camp says ". . . He may then struggle for some time with one foreleg vibrating vigorously in the air and the other pawing for a foothold in the ground before he can right himself."

Our observations lead us to believe that it would be a very unusual condition if the tortoise failed to right itself from such a position. The behavior pattern begins with movement of front legs to feel the ground, whereupon it pushes with one leg and pulls with the other.

If the feet cannot get proper anchorage, additional efforts follow. One front foot swung violently through the air serves to move the shell around and a new trial is made. If this also fails, a final resort may bring the head into use. It is stretched forward as far as possible and then pushed against the ground upside down so that it rocks the shell on the carapace to one side whereupon the front foot on that side

has a better chance to get a firm hold and usually results in righting the tortoise (Fig. 14).

It is probable although it has not been observed, that a coyote might turn a tortoise over on its back and leave it that way if it could not penetrate its passive defense. Tortoises left by predators on their backs would be almost certain to turn over unless in very unusual circumstances where the shell became wedged in rocks or was left lying on hard bare ground where it could not get a toe hold for its front feet. Perhaps a tortoise weakened by parasites or disease might be too weak to make the effort to right itself from the upside-down position. In all probability a high-domed tortoise like *berlandieri* would find it easier to turn over than would a low-domed tortoise like *agassizii*.

Six tortoises, during the course of these studies, have been found dead lying on their backs under conditions that arouse suspicion that they may have died in that position. Tortoise 3♀ was found dead on April 8, 1939 within a few feet of where she was last seen alive on March 25, 1939. The other tortoises on their backs were found as follows: unbranded, in left fork of Don Den, December 17, 1939; same tortoise in same place, February 20, 1943; Unbranded, between Alpine and Cove dens, November 30, 1940, partly eaten; A2♀, carapace only, 30 feet north of Overhang Den, December 8, 1945; unbranded in Yucca Wash near Yucca Den, December 8, 1945; unbranded, Mouth of Joshua A Den, December 8, 1945.

MOBILITY

The lack of speed of the tortoise is almost proverbial and perhaps justly so, but the animal exhibits somewhat surprising agility when faced with the necessity of avoiding the dangers of overheating or when eluding an enemy. Tortoises removed from dens and placed near the entrance have often been able to extend their heads and legs and scuttle to the safety of distant parts of the tunnel before their escape could be prevented.

The velocity of a large male tortoise was measured at Dixie Junior College, April 24, 1946. The cloacal temperature of the tortoise was taken before each observation. The animal was then placed in the direct sunshine and when he began to walk, the time that it took to travel over a measured distance was taken with a stop watch. The results are shown in Table 4.

According to this the tortoise would travel from 720 to 1584 feet each hour, or it would take from 3.3 to 7.3 hours to travel one mile. It is likely that slightly greater speeds could be obtained. The higher temperatures, provided the lethal limits are not approached, apparently would produce higher speeds. However, a tortoise would not likely maintain a constant speed for any length of time, nor would

FIG. 14. View of tortoise struggling to right itself from upside-down position. Courtesy of California Academy of Science.

TABLE 4. Speed of tortoises.

Original temperature	Distance moved (in feet)	Time in seconds	Velocity (feet per second)
28.5°C (83.3°F)	9.0	37.0	.25
29.5 85.1	6.3	28.5	.22
32.0 89.6	9.0	45.0	.20
32.5 90.5	19.5	48.0	.40
33.0 91.4	14.3	32.0	.44

the line of travel even approach a straight line for any great distance.

One particularly interesting incident may show the mobility of a tortoise under unusual circumstances. On May 6, 1939, a large animal was captured on the flat northwest of Point Den between Den and Dugway Washes. It was unbranded, and since all branding equipment had been left some distance away, it was loosely tied in a large cloth flour sack, and left in the shade of a Joshua tree while awaiting a return with the branding iron. Upon return, a short time later the animal had completely disappeared. Detailed searching of the entire neighborhood failed to reveal either the tortoise or the sack. November 30, 1940, the riddled remains of a large cloth sack, evidently the same one, was removed from Cove Den about a quarter mile distant from the original capture.

Tortoises have some climbing ability, judging from the dens which they enter. Many of the winter hibernation places are at the top of a steep bank. High Den is located beneath such a steep gravel bank in a position so that a tortoise approaching from the bottom of the wash would climb 51 feet at an angle of about 45 degrees, climb a vertical gravel ledge which is 12 inches at its lowest place and then go an additional four feet at an angle of about 40 degrees. Tortoises have frequently been found in this den even though the tunnel cannot be entered except over the vertical approach mentioned (Figs. 15, 17).

At Jump Den, tortoises must climb sixteen inches; four inches of which lead to a narrow platform, possibly large enough to accommodate the hind feet, above which a vertical ten inches lead up to another two-inch slope which must be climbed before this frequently used den may be entered.

In spite of its reputation of being a slow stay-at-home, the tortoise's ability to travel and climb undoubtedly is an important adaptation which aids it in its struggle for survival.

As would be expected, it is poorly adapted to life in water. Its only contact with water is rain or periodic floods. When placed in deep water, it floats with the dome of the carapace projecting above the surface and head and legs submerged. When it attempts movement, the leg motions are very awkward for swimming but they do result in some locomotion.

When it attempts to breathe, it pushes the head outward and upward toward the surface, which is very difficult to reach with the nose. In some cases, it requires additional movements of the legs. In any case, it requires a strenuous effort to get the head into a position to breathe. Long continued floating would doubtless result in tiring the tortoise to the point where drowning would ensue. A tortoise was found dead in a water pan at Dixie College under conditions which suggested drowning in this fashion.

FIG. 15. View of east side of Den Wash showing location of High and Hillside dens in gravel bank at top of slope; *Yucca baccata* and desert almond in foreground.

FOOD

All available data point to the idea that the desert tortoise is primarily vegetarian. Pope (1939:244) includes insects and dried rabbit meat in the diet of items eaten in captivity, but we have found no corroboration from observations in the field. However, it is entirely possible that insects might be ingested on the plants that are eaten, especially in flowers.

Grass appears to make up the greatest bulk of the diet. Our records show that tortoises were observed eating grass on September 30, 1939, November 23, 1939, January 18, 1941 and October 28, 1945. The grasses were identified as mesquite grass, and cheat grass, *Bromus rubens*. The Ortenburgers (1927) found only grasses in the stomachs of tortoises they examined in Pima County, Arizona according to Pope (1939:242).

A tortoise was observed eating alfilaria on January 18, 1941. Miller (1932:196) states that on the desert they crop the heads of a composite flower, *Encelia canescens*, and doubtless would take any other fresh vegetation. Woodbury (1931:122) suggests that they probably live on green succulent desert vegetation when it is available.

It is obvious that the tortoise must have adapted its food habits to the conditions under which food can be obtained. The small shrubs of the desert which the tortoise can reach are mostly woody or tough but most of them produce tender buds or flowers during periods of growth, mainly in early spring, but there is lesser growth, especially of flowers in the fall.

The lush carpet of annuals that usually fills up the spaces between the bushes in early spring and sometimes in fall offer a great variety of green succulent vegetation, probably rich in vitamins, when it is available. It is normally limited to a 30- or 40-day

period in spring and in fall but when the sheep herds sweep the carpet clean the tortoise access to the fresh green vegetation is limited to a few days.

The mesquite grass which grows up through many of the bushes and which the sheep do not decimate seems to be the chief source of food for the tortoises. Being protected by the bushes and not particularly palatable to sheep, it grows up and dries in place and often persists during the drouth periods.

This mesquite grass is available at almost any time of the year although it is green and fresh in the spring and sometimes in the fall, but is dry and coarse during the remainder of the season. Tortoises have been observed eating it in September, October, November, and January. Mesquite grass, also called Bush Muhly, is reported by Hitchcock (1935:381) to be found on "dry mesas and hills, canyons, and rocky deserts," from "Western Texas to Colorado, Nevada, and southern California, south to northern Mexico." It thus seems to be found throughout the range of the desert tortoise and beyond into the area occupied by Berlandier's Tortoise.

The hypothetical diet of green herbs and flowers when available is based largely upon diet eaten in captivity, where under artificial limitation of foods they are known to eat great varieties of grass, vegetables, fruits, flowers, buds and leaves of many kinds of plants that do not occur on the desert.

Occasionally, however, in captivity, a tortoise refuses to eat anything and continues on to starvation. One specimen at the University kept by Dr. Schell refused to eat anything until tempted to taste pink peach blossom petals after it had been noted dabbing its mouth toward a pink blotch of color on a dress. Thereafter, it ate many things that had been previously rejected. Other tortoises have been noted which appeared to have special preference for yellow and responded by eating yellow dandelions. Probably it has a well developed sense of color. This diet in captivity has been discussed by Woodbury (1931:122), Miller (1932:196), Pope (1939:244) and others.

Of several specimens that have been dissected all have shown in the large intestine coarse fibrous plant material mixed with finer green material resembling the softer portions of leaves. Much of the fibrous material can be identified as grass stems, doubtless *Muhlenbergia porteri*. The large intestine is usually distended with such material, even during hibernation.

In captivity as well as in the dens when in hibernation, tortoises go long periods without defecation, probably as much as six months when temperatures are low. It is entirely probable that little or no digestion takes place at this time. It also seems probable that enzymes are not being secreted under these temperatures. If so, the temperature threshold at which digestion becomes active needs further investigation.

The nema parasites which inhabit the large intestine apparently persist through low temperature periods when digestion is quiescent. Dr. Margaret Schell of the University of Utah has made the interesting speculation that these nemas may play a part in the transformation of the plant remains in the intestine into animal products which are digested when the worms die and thus furnish an important source of protein for the diet. This hypothesis needs further investigation.

Tortoise droppings nearly always contain some of this coarse grass fiber from the intestine. The pellets are about one to three inches in length and are usually tapered at each end. Dr. Schell has been able to demonstrate the presence of nema eggs in all droppings that she has tested.

The adaptations of this tortoise with reference to its food supply include the ability to survive on a diet which includes fresh green vegetation when available in spring and fall, coarse dry vegetation during the summer, and storage of fat for winter hibernation. The reduction or suspension of digestion during the winter poses questions of the control of nemas and bacteria in the digestive tract that have not been answered.

WATER

"There is hardly a more intriguing or less understood problem of the arid regions of the world than that of the means by which some of the animals of these areas exist without visible sources of water supply" says Vorhies (1945:487). Our studies have shown that a tortoise lives on a very small home range in a desert area where water is not available and does not depend upon drinking to supply its needs for water.

Babcock (1912) states that "Water is essential to life and during the period of development it is the most abundant constituent of living organisms, its amount ranging from about 40 to nearly 100 per cent of the total weight. Some of this water is imbibed directly, some of it is taken with the solid food which is rarely dry, and some of it is formed within the organism by metabolic changes in the organic constituents of the food and tissues, induced by respiration and other vital processes. The relative amount of water derived from each of these sources depends upon the kind of organism, its period of growth, the nature of its food, its environment, and its activities."

Baldwin (1940:43) gives the following values for the production of metabolic water by the oxidation of 100 grams of each of the foods: protein, 41.3 grams; carbohydrate, 55.5 grams; fat, 107.1 grams. It is known that the tortoises tend to store fat for winter and that it is a potential source for a large quantity of metabolic water when used. It seems probable that fat is produced during spring or fall when succulent green vegetation is available. It can then be utilized during either hibernation or estivation.

This tortoise is one of the animals which has reduced the intake of water by drinking to a minimum. Not that it will not drink but rather it does not get the opportunity very often. Miller (1932:196) reports examples of tortoises that produced increases of 41 and 43% in weight by drinking.

The infrequent floods, sometimes years apart, would furnish the only opportunities for drinking to tortoises on the Beaver Dam Slope. This flood water is always muddy, but sometimes settled pools occur after the floods subside. There is no evidence, however, to indicate that the tortoises are concerned for drinking purposes either with the floods or the pools and the tortoises continue to persist whether the floods occur or not.

It is obvious that the tortoise supply of water comes from food or from metabolic water which is indirectly derived from food. It is easy to understand how a tortoise could obtain a large supply of water from the lush succulent food of spring or fall, but it is more difficult to account for an adequate supply of water in the food during the long hot dry summer when it consists largely of dry mesquite grass.

This long dry period of summer is the most critical time of year for maintaining an adequate water content of the body. It is the period when greatest water loss from the body might occur by evaporation, and when the least intake of water in the food would be expected. Doubtless, the tortoise adaptations must be able to function under these extremes.

The tortoise appears to meet these extremes by two methods: by reduction in water loss and by production of metabolic water. The latter problem has not been studied by us experimentally, but the fact that its food contains large quantities of carbohydrates and that it stores much fat which needs only to be oxidized to release quantities of water is circumstantial evidence indicating the metabolic production of water.

The reduction in water loss results partly from morphological conditions, partly from physiological functioning and partly from behavior patterns. The horny plates of the shell, the scales and cornified skin of the rest of the body which are waterproof, reduce evaporation from the external surface of the body to a minimum.

This limits the areas from which evaporation can proceed easily to the internal surfaces of the respiratory tract. These internal respiratory surfaces lose moisture largely in proportion to the temperature of the tortoise and to the relative humidity of the air it breathes.

This respiratory evaporation takes heat from the body and lowers the temperature, but the total heat used and the total water evaporated are very small compared with that which would be lost if similar evaporation took place through the skin. Further ramifications of this problem will be discussed under adaptations to temperature.

As is well known, the relative humidity of air containing a given quantity of moisture varies inversely with the temperature. Despite the arid climate and the low quantity of moisture in the air, the great changes in the daily temperature rhythm bring high relative humidity when the temperature is low even though the relative humidity is extremely low when the temperature is high. At times of the day, when temperature is high and humidity low and the greatest danger of moisture loss is imminent, then an adaptation in the form of a behavior pattern provides for a reduction of moisture loss to a minimum.

In the morning, when evaporation is rapidly increasing, the tortoise descends underground into its summer hole about 3 feet below the surface where the soil is slightly moist and where the relative humidity is maintained at a relatively high level. Some moisture from the lungs is added to the atmosphere in the hole, increasing the amount in the air and retarding further evaporation. It is thus able to maintain itself in an atmosphere of high humidity at all times and reduce its moisture loss from respiration to a point that will allow maintenance of a necessary water balance in the body.

A further reduction in water loss results from physiology of excretion. The large bilobed urinary bladder, in all cases dissected, contained large quantities of solids held in suspension in a large quantity of water. Tortoises disturbed in the field often discharge part of this water, which is clear with a pale brown color.

In captivity, tortoises go long periods, weeks or months, without making such discharges of water. There is evidence from our observations to indicate that this is true in the field, also. The chief function of this water appears to be a vehicle for holding the urinary wastes which are stored in the bladder mainly as insoluble uric acid or its ammonium salt precipitates.

The function of this water has been variously interpreted. Cox (1881) after dissecting a specimen reported finding a large membranous sac on each side filled with clear water. Bailey (1928:372) refers to one of these tortoises which he picked up as crawling into its shell so tight as to squeeze out half a pint of clear, clean water. Later, he says that the bladder of one saved for a specimen contained nearly a pint of clear water. "As has often happened in the Galapagos Islands where a turtle is squeezed and a drink of good water obtained where no other fresh water is to be had, a good (sic) drink that might save human life could invariably be obtained from one of these tortoises."

Whatever is thought about the idea of drinking turtle urine, it is doubtless a fact that it could be obtained at almost any time from a tortoise. Miller (1932:201) states that "Urea is produced by mammals, while uric acid or its ammonium salt is the corresponding product of birds and reptiles. Urea is soluble and highly toxic, hence must be eliminated at the expense of much solvent water before its concentration becomes too great. Uric acid, on the other hand, is almost insoluble, hence less toxic, and is voided as a whitish solid by the reptile and a minimum of water is lost."

An analysis made for us by Dixon M. Woodbury showed that the great quantity of whitish solids in the urine of the tortoise bladder was mainly uric acid. Whether small quantities of other urea derivatives were present was not determined.

TEMPERATURE

Terrestrial ectothermic animals of the temperate zone have a serious problem of maintaining suitable body temperatures and this is greatly accentuated in deserts where there is great variability, both daily and seasonal. It is well established (Borradaile 1923: 23, Belehradek 1935:2) that the rate of chemical activities of living organisms varies with temperature, having an optimum range in which protoplasm operates most effectively, below which the rate reduces to a minimum where it may be stopped by freezing of its water and above which it also decreases to a maximum temperature where it may be brought to a complete stop by coagulation of certain proteins.

Inactivation in animals resulting from lowering temperatures between the optimum and minimum is usually called hibernation and inactivation resulting from rising temperatures above the optimum is sometimes called estivation. The extreme inactivation reached at the minimum is known as chilling or chill coma whereas that which occurs at the extreme maximum temperature where the proteins begin to coagulate results in paralysis. Inactivity of hibernation shows a decided gradient, doubtless correlated with lowering temperature, passing from active through lethargic and comatose toward rigid conditions.

Every animal must find within its environment temperatures within which its life processes are adapted to proceed smoothly enough to carry on vital activities. This is necessary not only for the development of eggs and young, but also for the maintenance of the normal processes of life for the individual. In many animals, this optimal range of temperature for smooth functioning which is called normal activity range by Cowles & Bogert (1944:277) is as great as the normal range of temperature in the surroundings either during the whole year or during the season of its activity (Borradaile 1923:25), but in the desert with its great variation in daily and seasonal rhythms, suitable temperatures within the optimum range do not occur continuously, but are broken by both the daily and seasonal variations into short discontinuous periods.

The heat necessary to protoplasmic operation is supplied mainly from the environment except in those cases where heat results from protoplasmic activities. This protoplasmic heat is almost negligible in most of the cold-blooded (ectothermic or poikilothermic) animals, but is exceedingly important in the warm-blooded (endothermic or homoiothermic) birds and mammals where the chemical heat energy derived from food is substituted for that derived from the environment.

Protoplasmic heat in the desert tortoise is usually low in quantity and its ordinary effect is to raise slightly the temperature that would otherwise be obtained from the environment. Heat from the environment is obtained mainly by (a) conduction from the ground, (b) radiation from the sun and (c) transmission from the air.

Heat is lost to the environment mainly by (a) radiation from the body into the air, (b) conduction to the ground if ground temperatures are lower and (c) by evaporation of water. The temperature of the body closely approximates the resultant of the gains from and losses to the environment.

As Cole (1943:100) has shown for lizards, it is probable that tortoises closely follow the temperature of the ground upon which the body rests. It is well established (Smith 1929:83, Vorhies 1945:502) that soil surface temperatures vary a great deal more than the air temperatures. This is, of course due mainly to the differential heating effect of sunshine upon the two media.

Sunshine passes through the air with slight loss of radiation by heating some constituents in the air, notably water vapor and dust. That part of the sunshine which survives passage through the air is stopped immediately at the surface by the ground or by the plants that shade the ground.

In the desert where so much of the ground is exposed, the concentration of much radiant energy at the surface raises the top soil temperature to extremes that are far above both the air and the maximum lethal temperatures of reptiles (Cole 1943:97, Cowles & Bogert 1944:287). This soil then reradiates heat into the air and at night when there is no radiant energy being absorbed, it cools down approximately to match the temperature of the air.

Since the tortoise temperature is tied so closely to that of the soil on which it rests, it would be subjected to much greater variations than those recorded for air temperatures if it remained on the exposed surface of the ground all the time. It has two methods available for avoiding the uncomfortable or lethal temperatures of exposed soil—move into the shade of plants or go underground.

In a desert such as that on the Beaver Dam Slope, the widely spaced plants protect only about 25% of the soil surface. Their presence intercepts much of the sunshine that would otherwise reach the soil surface and thus prevents unduly high temperatures in the shade. The soil temperatures of the shade tend to approximate the temperatures of the air although there is some lag in adjustment between the two and there is doubtless some influence by conduction from adjacent sun-drenched areas.

Escape into the shade would occur largely at a time when soil temperatures of the shade are within the normal activity range of the tortoise and those of sunny areas were within the uncomfortable zone above the optimum. There would be little incentive for a tortoise to move into the shade from areas that were below the optimum.

The recourse to underground shelters occurs when neither sun-drenched nor shaded areas offer temperatures within the normal range of activities. This occurs mainly at the seasonal temperature extremes in summer and winter and in daily temperature extremes in the heat of day or the cold of night.

These problems involve the relationship between surface and underground temperatures. A general picture of these relationships at Davis, California

has been given by Smith (1929:83) and in the southern Arizona desert near Tucson by Vorhies (1945: 499), in which the details differ, but the general principles of these relationships are clear (Fig. 20).

The soil which is warmed by the sunshine in the daytime cools off at night. The process is repeated next day. In the meantime these changes are started downward through the soil by conduction, but the temperature is gradually reduced as it proceeds. Thus, daily temperature waves which gradually lose their intensity proceed rhythmically downward. At 2 to 4 feet, the day and night peaks are nearly lost.

The temperature at which the daily waves start varies from season to season, being extremely high in the summer and low in the winter. Ordinarily the underground temperatures are cooler in summer and warmer in winter than the surface. In other words, the peaks of the surface are reduced by lag and attenuation to mere bulges or slight deviations a few feet underground. The temperature becomes progressively more stable at greater depths and our records show the curve to be a straight line at 17.5 feet inside a den.

Even though the tortoises are driven to underground shelters in both summer and winter, the behavior pattern responses are very different in the two cases. They resort to the temporary holes (page 184) in summer and to the permanent horizontal dens (page 181) in winter. The response in each case is doubtless an adaptation which leads in the direction of finding comfortable situations.

Summer holes are used at a time when necessary to escape from uncomfortable or lethal high ground temperatures; dens when necessary to escape from uncomfortable or lethal low ground temperatures. The holes are used primarily for short periods of time—periods that fit the daily rhythm. The dens are used for long periods of time that fit the seasonal rhythm.

In the temperate zone, ground temperatures within the comfortable normal range of activity of tortoises are more common in spring and fall than at other times. At that time, tortoises can usually find comfortable ground temperatures in either the sunny spots or shaded areas, by shifting from one to the other without resort to underground shelter. It seems probable that they might endure slightly uncomfortable temperatures for short periods of time such as might occur on a cool night or a warm day without attempting to go underground.

In the summer, ground-surface temperatures in mid-day usually exceed the comfortable range even in the shade, but especially in the sunny portions where they often go far above the lethal maximum. At night, however, such temperatures generally descend to points well within the comfortable normal range of activities.

In summer, when it is necessary to avoid high temperatures only part of the day, the behavior pattern adaptation does not usually drive them to seek the protection of the winter den tunnels although occasionally one wanders into a den if it is near. The urge for shelter under these conditions usually results in the tortoise entering a summer hole if one is available or in digging a new hole if necessary.

Such holes are usually repaired or new ones dug in the early part of the summer and thereafter are available for use during the rest of the season. Occasionally new holes are dug later in the season. Just how much stimulation from uncomfortable conditions is necessary to initiate the digging is not known, but observations on tortoise Be♂ on July 15, 1939 when the days were hot and the nights were cool are illuminating.

This tortoise had been afield during the night. As the sun mounted and the ground began to warm, tortoises generally began to move toward holes. Others were observed to enter holes before 10 A.M., but this one passed by the hole it occupied the day before without entering and proceeded northwest about 100 feet directly to an old hole that recently had been nearly filled with dirt from rodent burrows.

It could not enter the hole, but rested across the top of the fill for a few minutes. Ground temperature and doubtless the tortoise temperature were rapidly rising at this time of day, and it was not long until the tortoise began to move again toward another hole in the same general direction about 100 feet distant. It reached this by a circuitous route and tried to enter, but it too was partly filled with rodent burrowings and was not deep enough to give adequate protection.

It rested a few moments and then started to repair the hole, digging at the bottom and pushing dirt out to the top. This did not continue very long. The tortoise soon stopped digging and wandered off directly toward another hole about 60 feet farther in the same general direction, which was open and which was entered at once, about 10:15 A.M.

At a time when air temperatures were rapidly rising and ground-surface temperatures were soaring, this tortoise had been balked in its efforts to enter two holes and finally found refuge in a third, at which time, it was breathing rapidly and gave indications of distress. The digging for safety in the second hole had been abandoned in favor of an attempt to find an open hole. Apparently the tortoise was familiar with its geography and knew the location of holes.

This tortoise had entered a hole which had a much lower temperature at the bottom and doubtless its temperature was soon adjusted to that of its environment. It remained in this place all the rest of the day—an indication that it was in a more comfortable situation than it had been on the surface before it entered.

This response, however, may not have been entirely an effect of temperature. The problem of water supply may have have had a bearing. The rapid breathing indicating distress and used as a method of cooling was doubtless depleting the water content of the tortoise at a much higher rate than normal, which in turn was another danger threat if unduly prolonged.

This daily behavior pattern tends to vary with the progress of the season. In spring, excessive ground temperatures begin to appear in early afternoon for short periods of time. Later, they appear progressively earlier in the day for longer periods, until by mid-summer, tortoises leave the holes sometime during the night and return the next morning usually before 9 or 10 A.M. During the remainder of the season, this process is reversed until by September or October there is small need for the holes.

After the comfortable fall temperatures begin to wane, the night temperatures drop below those of the tortoise's normal range of activity. When these drops at night are sufficiently severe, a behavior pattern appears to be triggered which sends tortoises to the winter dens. The scatter graph, Figure 16, indicates that this occurs about the second week in October and that they remain in the dens until about the second week in April, a six-month period.

Available evidence indicates that the majority of tortoises remain in situ during this time, but a few emerge temporarily on warm days and sometimes enter other dens. A single tortoise in each case was observed outside the dens eating grass on November 23, 1939, January 18, 1941 and October 28, 1945. For other records of tortoises that have moved during the winter, see page 186.

During their long stay underground especially in long dens, some tortoises move around and are not entirely comatose, but are rather more or less lethargic. Others, especially in shorter dens, become more or less comatose and probably move but little. An unbranded tortoise was found in a comatose condition on March 6, 1946 in a den that had been blocked by a woodrat nest which prevented it from entering further than seven feet.

Tortoises removed from dens and set on the ground in the sun on November 27, 1937, remained inactive until their temperatures had increased in the neighborhood of 15 or 20° F. to 85° F. when air temperatures were 71° F. before they became active. Similar results were obtained on February 17, 1946, when body temperatures rose about 19° F. to approximately the same level before they became active. This indicates that they were hibernating at temperatures much below the normal range of activity.

Often during the long period of hibernation, daytime temperatures rise above those of the dens even though the night temperatures are much lower. Since the den tunnels are nearly horizontal, outside temperatures would be transmitted inside to the tortoises much more easily than if there was a definite rise inside the mouth which would trap warm air and tend to prevent cold air from entering.

The farther tortoises are inside the den, the longer will be the delay in transmitting outside temperatures to them. Those that are near the mouth are doubtless stimulated much quicker than distant ones. Perhaps they are the ones that leave the den on warm days in winter.

Those farther in the dens might not be stimulated soon enough to take advantage of the warm day, or perhaps the stimulus might be so attenuated that it would be ineffective at distant points in the den. If it is necessary to raise the temperature of the tortoises 20° F. in the den as it is outside certainly the attenuated stimulus from the outside would be ineffective. This finds support in repeated experiments of placing tortoises from dens in the sunshine until they reached temperatures that stimulated activity. While beginnings have been noted in some tortoises as low as 59° F. (15° C.), yet there is a gradient

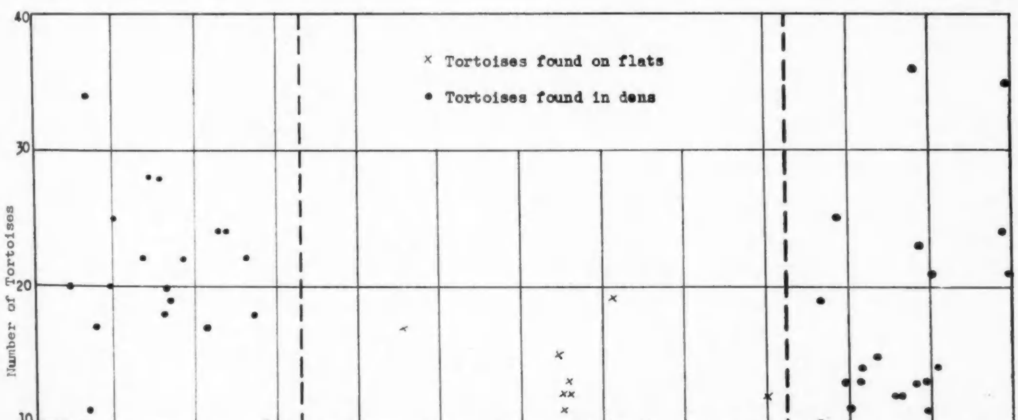


FIG. 16. A scatter graph showing time of occurrence of tortoises in dens and on the flats.

of increasing activity with increasing temperature until at about 80 or 85° F. (26.7 to 29.4° C.), all tortoises became very active.

As an explanatory hypothesis, it might be assumed that there is an hereditary cyclical rhythm that sends them into hibernation when stimulated to do so by lowering temperatures and brings them out in the spring when stimulated by rising temperatures. This hypothesis has some support from observations of tortoises in captivity, where they may be kept active all winter by temperatures of 75 to 80° F. or above, but may be sent into hibernation by temperatures below 60° F.

TABLE 5. Temperatures in relation to migration. This table shows in part the location of tortoises in dens and on flats as discovered on successive visits to the study area in relation to the maximum and minimum daily temperatures reported at the St. George Weather Station. The cross lines in the table represent the approximate period at which the shift in location takes place. This occurs at a time when the maximum temperature approximates the optimal activity range of the tortoise.

Date	Number of Tortoises			No. of dens visited	Temperature Range	
	In deep dens	In shallow dens	In holes and on flats		Maximum	Minimum
11/28/36	13	..	..	1	62	26
11/25/37	6	3	..	2	67	31
10/28/38	6	..	..	2	83	39
11/ 5/38	25	..	..	5	62	35
2/18/39	17	1	..	9	55	25
2/25/39	21	1	..	9	59	26
3/11/39	23	1	..	14	64	30
3/25/39	9	1	..	14	81	44
4/ 8/39	2	..	6	?	88	40
5/ 6/39	..	..	17	?	83	50
5/20/39	..	..	7	?	85	46
6/16/39	..	..	4	?	91	57
7/14/39	..	3	12	2	109	66
7/15/39	..	4	8	5	106	68
7/16/39	..	1	12	1	102	66
7/17/39	..	1	5	1	102	63
8/ 3/39	..	4	5	5	101	75
8/ 4/39	..	6	13	7	101	73
9/16/39	..	..	3	?	90	52
9/30/39	1	..	12	?	86	53
10/ 6/39	4	..	..	12	78	43
10/ 7/39	3	..	2	18	75	44
11/ 4/39	13	1	..	12	78	37
11/18/39	10	2	..	14	64	25
11/23/39	35	1	1	17	60	26
11/24/39	13	..	..	14	57	33
11/25/39	23	..	..	8+	69	33
12/17/39	5	..	..	3	57	26
12/27/39	6	..	..	6	41	11
12/30/39	34+	1	..	10+	60	24
12/31/39	21	..	..	2	63	27
1/ 6/40	8	..	..	20	50	25
1/20/40	11	..	..	15	47	23
2/10/40	22	..	..	5	57	27
2/17/40	27	1	..	9	61	27
3/ 2/40	9	..	..	6	65	34
4/ 4/40	4	1	..	30	72	40
4/ 5/40	0	..	..	12	74	39
4/ 6/40	1	..	2	1+	72	42
6/29/40	1	1	2	2+	89	72
7/15/40	4	1	10	4	99	66
7/16/40	2	4	8	4	90	70
10/19/40	8+	2	..	8	82	45
10/20/40	1	..	..	11	85	44
11/ 9/40	15+	..	..	2	60	32
11/30/40	20+	1	..	21	61	27
1/18/41	34	..	..	8	53	25
2/ 1/41	25+	..	..	12	60	31

Could it be possible that the tortoises are more comfortable in their lethargic hibernation in the even temperatures of the dens than they would be in excessive changes in the daily rhythm outside, and once ensconced in the distant portions of the dens, they are then protected from the temperature fluctuations outside and are not stimulated into activity by rising temperatures until the general temperature level (mean) rises in the spring?

During the operations of gathering and marking the tortoises from dens in Den Wash on October 28, 1938, air temperatures outside the dens ranged from 74° to 86° F. (23.3 to 30° C.). Thirteen tortoises were removed from dens in lower Den Wash and set in the sun. Some of the first tortoises removed yielded temperatures of 71 to 72° F. (21.6° and 22.2° C.), but the others were not measured. Some temperatures were taken from time to time. At 80° F. (26.6° C.), the tortoises were mostly inactive, but at 85° F. (29.4° C.) they tended to become very active. At 2:30 P.M., when placed in Hillside Den in the shade, all remained there except one active tortoise which came out and started across the wash in the direction of Big Den.

On March 11, 1939, air temperature outside at 12 o'clock was 57° F. (14° C.) when the temperature in Woodpecker Den was 50° F. (10.5° C.) and tortoise temperatures were 50° F. (10° C.). These readings were not quite simultaneous, but were near enough for close approximations. At 4:30 P.M., the air temperature was 62.5° F. (15.5° C.) inside the mouth of the den and a tortoise removed from a distant part of the den gave a reading of 53° F. (11.5° C.).

On March 25, 1939, a tortoise with temperature of 57° F. (14° C.) was removed from Woodpecker Den when air temperature at the mouth of the den was 62.5° F. (17° C.) and outside the den was 69° F. (20.5° C.). On December 2, 1945, when air temperatures outside were nearly 60° F. (15.5° C.), air temperature at 8 feet inside was 58° F. (14.4° C.), about 11:00 A.M.

On May 6, 1939, when tortoises were inhabiting summer holes, air temperatures at 11:20 A.M. read 81.5° F. (27.5° C.) in shade and 86° F. (30° C.) in the sunshine (thermometer shaded). On this date, one tortoise was found in a summer hole at 7:30 A.M., two others were out of their holes at 8:30 and two additional tortoises were found on the flats at 10 A.M.

On July 14, 1939, a tortoise was found on the flat southwest of Big Den at 7:30 A.M. in the early morning sunshine. By 8:45, when air temperatures were beginning to soar, it moved over to its summer hole about 20 yards away and entered. At the time of

entry, its cloacal temperature registered 100° F. (37.8° C.).

On September 30, 1939, a tortoise was first found in the shade of a Joshua tree on the low ridge east of Den Wash opposite Overhang Den. At 12:30 P.M., air temperatures were recorded as 90° F. (32° C.). About 45 minutes after it was first seen, it was found in the shade of another Joshua tree in the bottom of Den Wash near Overhang Den about 50 feet distant from the first tree. It had doubtless moved from one shady spot to another over ground that must have had temperature much over 100° F., but being propped up on its legs when walking it would be exposed to air temperatures and sunshine, but not to conduction from the ground.

Eight tortoises removed from Dugway Den on the afternoon of February 17, 1946 had cloacal temperatures of 53.8° F. (12° C.) at a time when air temperature near the point of hibernation, 17.5 feet within the den, was 55.4° F. (13° C.) and that at the entrance was 57.1° F. (14° C.). All were set in the sun on warm gravel. Three of the eight showed initial activity (moving head or starting to walk) after 33, 38 and 46 minutes, respectively, when cloacal temperatures were 60.8° F. (16° C.), 59° F. (15° C.) and 62.7° F. (17° C.). The balance had shown no activity at the time they were returned to the den although one that had been exposed longest (111 minutes) had a cloacal temperature of 72.5° F. (22.5° C.).

UNDERGROUND SHELTERS

Two kinds of underground shelters are utilized by the tortoises—dens and summer holes (Fig. 21). The dens are horizontal tunnels driven in banks of washes, usually for distances of 8 to 15 feet, occasionally as much as 20 or 30 feet, whereas the summer holes are scattered over the flats and benches and are sunk from the surface downward at angles from horizontal of about 20 to 40° for a distance of 3 or 4 feet.

DENS

The dens are more or less permanent affairs that are re-used year after year for winter hibernation. Doubtless, slight changes are made from time to time and probably such slight alterations result in gradually lengthening the tunnels. Even though no tortoises have actually been observed at work, yet definite changes in the internal arrangement have been recognized and there is little doubt that the tortoises were responsible for most of them. Many tortoises have been found that had entered and piled up dirt behind them in the tunnel. The work of wood or pack rats is readily distinguished from that of the tortoises.

A few of the dens have large cave-like openings but these usually have small tunnels leading backward from the rear. The openings of most of the other dens were small half-moon shaped affairs like that described for Big Den. See Fig. 17. Some of these dens with small openings have material piled outside below the opening doubtless derived from ex-

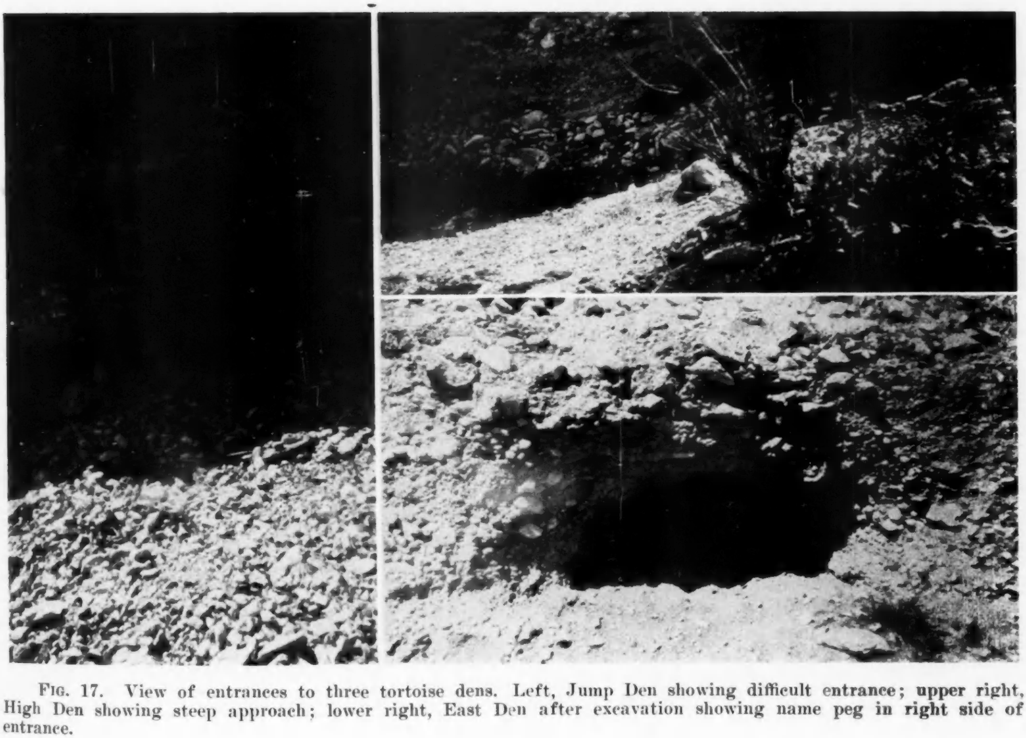


FIG. 17. View of entrances to three tortoise dens. Left, Jump Den showing difficult entrance; upper right, High Den showing steep approach; lower right, East Den after excavation showing name peg in right side of entrance.

cavations within. The forms or shapes of the dens vary a great deal. No two are exactly alike, but all have a similar architectural pattern. The diagrams shown in Figures 18, 19 show some of the differences in form.

Since these dens are used for winter hibernation, they must offer some protection against the inclement weather which often goes below freezing in winter. The mouth of the den being open, allows air to circulate, but there is a prolonged lag in equilibrium between outside air changes in temperature and those within the den.

This lag produces a much more even temperature within the den than the greatly variable temperature of the desert outside, where daily fluctuations often reach 40° F. and sometimes reach extremes of 50 to 60° F. in winter. The daily range within the den is much less than this. The effect is to cut off the peaks and maintain a temperature which tends to approach the outside mean (Fig. 20).

The temperature within the den is further modified by contact with adjacent soil surrounding the air in the den. The soil acts as a reservoir, absorbing heat from the air when air temperature is higher than that of the soil and releasing heat into the air when temperatures are reversed. This tends to stabilize still further the temperatures of the den.

Cole (1943:100) has shown for lizards that they are more affected by the temperature of the sand upon which their bodies rest than by the temperature of the air surrounding their bodies. In no case did he find warm air heating lizard bodies faster than it heated the sand. This is in accord with the principle of physics that in general, solids with their compact molecules are better conductors of heat than are gases with their dispersed molecules.

The same principle doubtless applies to tortoises. In the dens, they would tend to maintain the temperature of the ground on which they were resting rather than the changeable air of the dens. The ground temperatures within the dens would be resultants from two sources: soil-conducted heat from the surface and air-transmitted heat from within the den, but there would be no direct effect from radiant energy of the sun.

This stabilizing effect produced by the lag and the soil is more pronounced farther inside than near the mouth. There is a definite gradient toward more and more stabilization running from the mouth inward. The longer the den the more stable the temperature at its distal end. This is illustrated in Figure 20, where thermograph records are shown that were taken outside and at various distances inside East Den.

The lag in equilibrium would theoretically be affected by the size of the opening, the smaller it is the greater the lag and conversely, the larger the opening the quicker would outside temperature changes reach the tortoises within. The enlargement of den openings in the process of removing tortoises would doubtless permit quicker transmission of temperature changes from the outside and result in greater fluctuations of both air and soil temperatures within the dens. Woodrats frequently fill all or part of the den entrance or part of the tunnel with rubbish. This would aid in stabilizing the inside temperatures because it would diminish the air circulation.

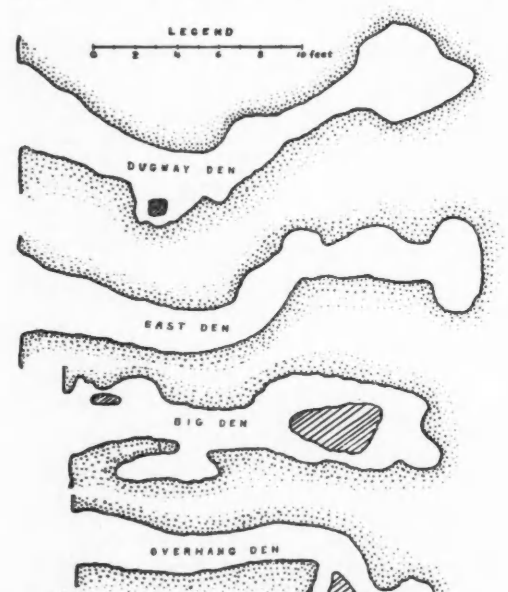


FIG. 18. Sketches of ground plans showing variations in size and shape of typical dens.

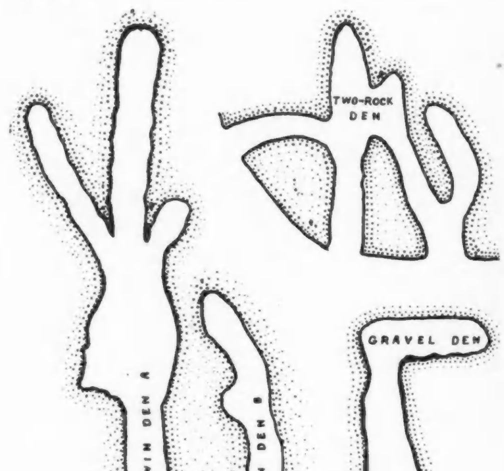


FIG. 19. Sketches of ground plans showing variations in size and shape of typical dens.

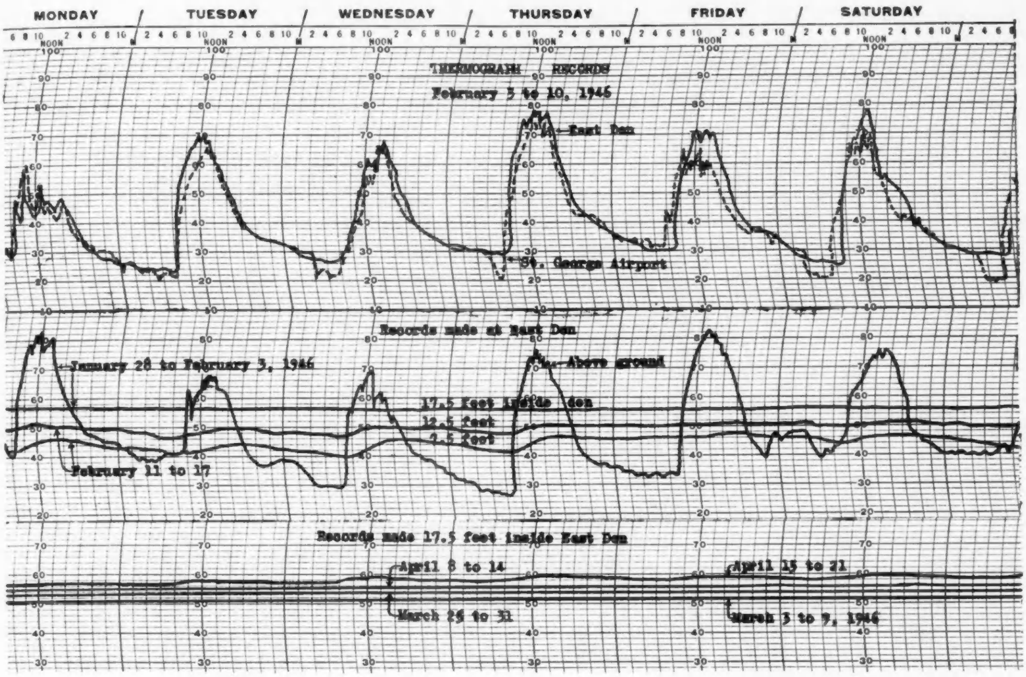


FIG. 20. Thermograph records. Upper, a comparison of temperature records at St. George Airport, 3,050 feet altitude and at East Den on Beaver Dam Slope, 3,300 feet. Center, comparative temperature records outside and at varying distances within East Den. Lower, comparative temperature records at a point 17.5 feet within East Den between March 3 and April 21, 1946.

The thermograph records taken near or within East Den, Fig. 20, at 7.5, 12.5, and 17.5 feet, respectively, from the mouth show successive smoothing of the curves of daily fluctuations until the last one at 17.5 feet is practically a straight line, which during the week of January 27 to February 3, 1946 dropped from 57° to 56° F. (13.9° to 13.3° C.). Three tortoises were hibernating beyond the place where the farthest record was taken.

A comparison of these thermograph records reveals not only a smoothing of the curves but also a lag and a steady climb in the mean temperature of each curve. The curve at 7.5 feet inside the den varies around 42° to 44° F.; that at 12.5 feet around 48° to 50° F. and that at 17.5 feet drops from 57° to 56° F. In the summer, this would doubtless be reversed and there would be a steady decline in gradient inside the den.

According to the thermographs, the temperature 17.5 feet within East Den dropped from 57° F. on January 28 to 51° F. on March 3, 1946. Thereafter, it rose slowly for the next six weeks at the average of 1° F. per week until it again registered 57° F. on April 15. During the next week, slight daily fluctuations involving as much as 3° F. increase over the preceding week appeared in the record. Two of three tortoises hibernating in this den until April 8 had left before April 21 (Figs. 16 and 20).

Of the 95 dens on the area, 50 were straight tunnels without any deviations of consequence. Twelve other dens had approximately right-angled bends in them, 6 turning to the left and 6 to the right. Two other dens had two major bends in each tunnel—Red Peak and East dens. Twenty-two dens were of irregular construction with irregular bends or branch tunnels. The balance were not recorded.

Of these same 95 dens, about 50 were more or less level throughout their length. Fourteen of the dens had a slight incline so that the inner end was slightly higher than the mouth, but 18 additional dens had enough slope so that the floor of the inner end was definitely higher than the top of the opening at the mouth. Four dens sloped downward so that the inner end was lower than the mouth, one of which, Vere Den, had the inner end conspicuously lower.

Many of the dens follow a given stratum of gravel that is exposed on the bank of the washes. Others do not; they follow the course set for the den regardless of the strata. Bends in dens would tend to prevent free circulation of air. The thermograph records indicate that circulation is much reduced inside until it is practically nil at the ends of long dens.

It seems reasonable to suppose that upward sloping dens would trap warm air at the inner end and downward sloping dens would trap the colder air, but the thermograph records seem to indicate that while

this might be true for shallow dens, the restricted circulation in long dens might prevent it.

East and Dugway dens are very similar (Fig. 18). They both face east. The former is about 22.5 feet and the latter 23 feet in length. They both make a left turn inside about eight feet from the entrance and then pass around a right turn to a terminal chamber. East den slopes upward so the terminal bend is about 2.5 feet above the entrance. Dugway den is approximately level. Air temperatures on February 17, 1946 read 60.8° F. (16° C.) at 11:45 A.M. at the mouth of East Den and 57.2° F. (14° C.) at 3:42 P.M. at the mouth of Dugway Den, but temperatures at 17.5 feet inside the dens at the times indicated, read 57.2° F. (14° C.) in East and 55.4° F. (13° C.) in Dugway. This temperature in East Den is only slightly different from that taken on the thermograph during the week of January 27 to February 3 already reported as ranging from 57° to 56° F.

SUMMER HOLES

The summer holes, in contrast with the permanent winter dens are more or less temporary affairs, sunk into the ground at convenient places on the summer range and are at least 4 times as numerous as the dens (Fig. 21). Occasionally a hole may remain undisturbed from one year to the next, but the great majority become filled by rodents or by other means and new ones are constructed as needed the next year.

The digging of such a hole has been observed only in part. The tortoise was first seen pushing dirt out of the hole in front of its shell which was being used like a scraper propelled by the hind legs. When pushed to the surface on approximately a 30° slope and over the edge of that previously piled, the tortoise turned slowly around and walked down to the bottom of the incline and began leisurely scratching the end of the hole with the front feet, first one, then the other.

The scratching continued over an arc a little longer than the length of the tortoise. After a pile of loose dirt was accumulated so that it interfered with operations, the tortoise slowly turned around and pushed the fresh dirt out to the surface.

Whether the hole is completed in one operation was not determined but it is probably extended as

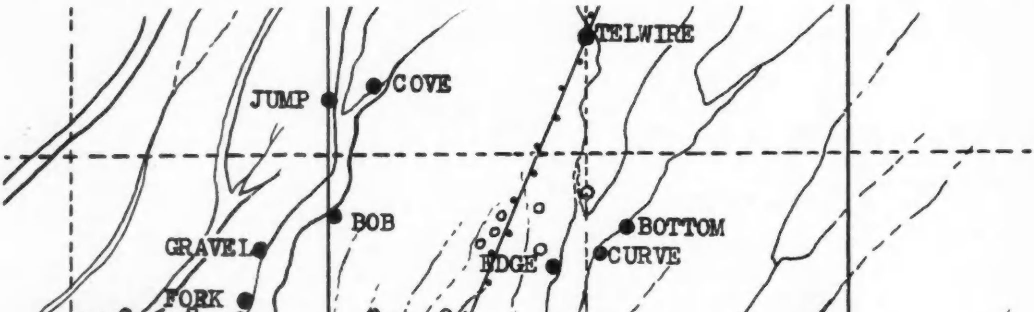


FIG. 21. Map of central portion of study area showing distribution of summer holes (open circles) in relation to winter dens (solid dots).

temperatures demand. The temperature of the soil in the bottom of the hole is the prime factor in determining the temperature of the tortoise. This temperature in summer depends mainly upon the amount of heat conducted downward from the surface, which in turn varies with the distance (Smith 1929:83).

The air in the bottom of the hole, being conditioned by contact with the soil, would in the daytime be cooler than the air above and there would be little tendency for the air to circulate. If, however, the night air temperatures dropped below that of the hole, then the warmer air of the hole would tend to rise and be replaced by the coolest night air, which would thus be trapped therein when outside air temperatures rose.

Summer holes occasionally last from year to year but the majority tend to become filled or partly filled between seasons. Weathering, wind and use by other animals all help in this process. Burrowing rodents in particular find such holes useful dumping grounds for the soil removed from their burrows. It is not uncommon to find them completely filled from this cause. In one unusual case, a jack rabbit was observed to use a hole for a shelter. On three occasions, when the hole was approached, the rabbit was observed to shoot out of the hole in a high leap into the air, probably having been warned by approaching footsteps. The trampling of sheep which cross over the area each spring, helps to cave-in the shallow parts of dens and throws dirt into the holes.

BEHAVIOR PATTERNS

Tortoises living in the desert are continually threatened with exposure to dangerously high temperatures in summer and to sub-freezing temperatures in winter. These constant dangers must be avoided in order to survive. The tortoises have developed behavior patterns which enable them to survive in face of these dangers.

For man, an anonymous writer in the Lancet (1941:77) called attention to four types of heat problems: (1) hyperpyrexia or true heat stroke, (2) circulatory insufficiency which produces heat prostration, (3) electrolytic imbalance which is often associated with cramps and (4) dehydration or loss of water.

Our observations lead toward the belief that the tortoises of the desert are exposed to dangers similar to that of man, particularly to heat stroke and dehydration. The behavior patterns that have been developed to prevent or avoid exposure to such dangers appear to be instinctive. Instinctive behavior is unlearned, characteristic of the species and is biologically adequate; an inherited coordination of reflexes in which there is pleasure and satisfaction associated with inherited muscular and glandular functioning, according to Hunter (1942:166).

Adaptative specialization as stated by Russell (1941:729) rules through the whole life history of any animal and one aspect of the specialization is the adaptedness of instinctive behavior on the perceptual side. "Each animal species has an innate predisposition to perceive and act with reference to particular objects and events which alone have valence for it." He suggests that in many cases the suitable object is distinguished by means of only a few of its possible valent characteristics and because some biologically insignificant objects may possess these same signs, one may expect to find frequent aberrations in instinctive behavior.

It is to be expected that the instinctive behavior of the tortoises that leads them to avoid dangers such as heatstroke or dehydration is associated with perceptual recognition of heated soil, summer holes, winter dens or other phenomena that stimulate voluntary behavior accompanied by some sort of pleasurable satisfaction that develops avoidance rather than endurance. Such activity is in the nature of comfort-finding or even comfort-seeking.

COMFORT-SEEKING

In analyzing a biotop of birds, Corti (1941:544) indicated that in its struggle for existence, each bird tends to seek optimal conditions in each subdivision of the biotop, such as the sitotop or feeding niche, the hygiotop or general well-being niche, and the genotop or breeding niche. This search for the optimum which he called the struggle for ease or avoidance of pain (disharmonic disquiet) and which he considered not necessarily identical with the individual's struggle for existence is more or less consistent with our idea of comfort-seeking in reptiles.

While comfort-seeking may be regarded as inherited coordination of reflexes that leads the tortoises to avoidance of dangers, yet there is ever present a threat that if they do not move in accordance with the reflexes there will be uncomfortable or even lethal conditions approaching, which in the course of evolution would tend to remove those that did not respond to the reflexes.

Such instinctive behavior is associated with both daily and seasonal behavior patterns that are characteristic of the members of the colony studied and may be hereditary in the species. These behavior patterns are primarily correlated with the temperature and moisture needs to avoid heatstroke and desiccation, whereas the feeding and breeding patterns are more or less subordinated.

The problem of reproduction involving mainly copulation and egg-laying requires but a few hours time per year and this is so adapted that it can be provided when temperature and moisture conditions are suitable.

The matter of nutrition is handled primarily by eating when food is plentiful in spring and fall, supplementing it with dry grass in summer and storing fat for use during the winter. Foraging, like copulation and egg-laying is timed to fit the behavior pattern when temperature and moisture conditions are propitious.

With no young to tend, copulation and egg-laying requiring only a few hours per year and foraging problems subordinated, the tortoises have most of their time available to adjust their behavior to fit the temperature rhythm.

It is conceivable that in years when there is a

scarcity of food, hunger might drive a tortoise out into temperatures beyond the range of the comfortable optimum, but when food is plentiful there should be no such necessity. If food were so scarce that the tortoise was faced with either starvation, heat-stroke or dehydration, it might prove serious and could serve as a population control mechanism.

Annual Behavior Pattern—Migration

The annual behavior pattern involves a short two-way migration, in which the tortoises inhabit the dens for winter hibernation where they utilize stored fat for nutrition, migrate to nearby ranges for summer where they utilize the summer holes to avoid heat-stroke and desiccation and then move back to the dens for winter. This is similar to a two-way bird migration, but the distances covered are approximately in proportion to their powers of locomotion.

This annual pattern drives tortoises into two different areas at different seasons of the year so it may be considered an adaptation to fit the seasons. The two areas although close together and overlapping are ecologically different. The dens are mainly in gravelly banks of washes and the summer holes are on the bench-like areas a few feet above the washes.

Not only are the areas different, but also the behavior is different in the two areas. In the dens, the tortoises remain dormant for months at a time without much activity. On the summer range, there is a daily behavior pattern evident and the tortoises are active for at least part of nearly every day.

There is a further difference in the approach to optimum comfort attained in the two areas. In the dens, the temperature seldom or never reaches that required for normal activities and the tortoises are continually subjected to temperatures that hold them in a lethargic or semi-torpid condition. This, however, is much nearer optimum than would be found outside. It may be interpreted as comfort-seeking even if comfort is not actually attained. It may still be interpreted as comfort-seeking even if hibernation comfort is on a different level from normal activity comfort.

On the other hand, the summer holes provide temperatures and moisture conditions that are definitely within the comfortable range. Being in shallow holes that keep the tortoises in close contact with external conditions of both temperature and moisture, they are then ready to emerge and become active whenever conditions are propitious. In spring and fall when conditions are suitable they may not even enter the holes.

Daily Behavior Pattern

The daily behavior pattern also follows a two-way movement, but on a much smaller scale even than the annual pattern. The daily pattern is inoperative during the winter except in the cases of tortoises that occasionally move about, but when they leave the dens during the mild spring temperatures, the daily pattern complicates the seasonal pattern until they return again to the dens.

In the early spring, they find comfortable conditions abroad during the daytime and seek protection from the cool or cold nights. A little later, when temperatures are higher, they are able to find comfort both day and night either in sunshine or shade and shift from one to the other as the daily rhythm demands. Still later, when it gets hot on the surface in the sunshine, then protection is sought in the summer holes in the daytime and activity abroad occurs at night or early morning. In the fall, the springtime march of the pattern is reversed.

While this pattern appears to be dominated by the struggle for temperature comfort, yet it also possesses elements that suggest a coincidental struggle for moisture comfort. Camp (1916:512) reported that tortoises come out of their holes after thundershowers. Such a phenomenon, which needs further verification, could be explained in three ways. First, during a heavy shower, water might run into the hole. Second, the temperatures of air and surface soil might be reduced to the point of comfort that would permit normal activity outside. Third, the air humidity might be increased to a point near the optimum.

It is interesting to note that both high temperature and low humidity that prohibit normal activity on a hot summer day would both be removed by the phenomenon of a summer thunderstorm and stimulate the search for comfort for both temperature and humidity outside of the holes, especially if further stimulated by hunger to search for its alleviation at the same time.

It is mainly the drives for temperature and moisture comfort that force tortoises into the summer holes during hot weather, but it is the hunger drive that appears to force them out nightly in search of food, thus producing the daily behavior pattern of movement from the hole to nearby range for food when conditions are propitious and back into the hole for comfort in the face of uncomfortable conditions on the surface. This is the picture of the daily pattern which modifies the larger annual pattern that drives tortoises from the winter dens to the summer holes and back again.

Even though tortoises normally enter winter dens in October and leave in April (Fig. 16), yet there is some movement during the winter. While we have actually witnessed tortoises moving outside the dens in winter only three times, it seems almost certain that the movements take place on warm days when outside temperatures are within the activity range. How they are stimulated into such movements is not clear.

The records disclose that a total of 56 tortoises have been recaptured during the winter after they had moved from one den to another. These were distributed as follows: 3 during the winter of 1938-39, 21 in 1939-40, 10 in 1940-41, 3 in 1941-42, 3 in 1942-43, one each in 1943-44 and 1944-45, and 14 in 1945-46. The low numbers during 1941-45 are due mainly to few visits because of war restrictions on travel.

During the same time, 96 tortoises were recaptured

2 or more times during a winter in the same den without moving elsewhere. These were distributed as follows: 16 in 1938-39, 33 in 1939-40, 16 in 1940-41, 2 in 1941-42, 18 in 1942-43, 3 in 1943-44, and 8 in 1945-46. Many additional tortoises were captured only once during a winter.

Of the 56 tortoises that were found to have moved during the winter, one moved from den to den 3 times during one winter; two had moved twice and the balance only once. How much the opening of dens and the disturbance of the tortoises during the process of recapture had to do with their movements is, of course, not known, but it is believed to be so important that without such disturbance there would be relatively little movement.

TERRITORIAL RELATIONS

Population

The area studied, embracing nearly two sections or about 1200 acres of land, represents the home area of a semi-isolated colony consisting of approximately 300 tortoises (Fig. 25). It is surrounded on three sides by steep foothill and mountain barriers at the edge of the range of the species, which appear to effectively isolate the colony from any contact with other tortoises in those directions.

It is only on the southwest that the way is open for effective contact with others, but even here it is very doubtful if any extensive intermingling with other populations takes place. Our studies of the surrounding region indicate several other such colonies occur in places where concentrations of winter dens are located in suitable wash banks.

The area to the southwest has few suitable places for winter dens and the population across the flats in that direction is very sparse. Presumably, the distance to the next colony is too great for regular effective interchange of members of the population.

This partial isolation enables the colony to be analyzed as a geographical unit, typical of many such units which there is reason to believe are scattered over the colder portions of the southwestern deserts. This does not imply that tortoises may not be sparsely scattered over other types of country, but rather, where suitable den sites are available in suitable quantities, then sufficient numbers of tortoises will be able to winter satisfactorily to keep the area fully stocked.

Summer holes can be dug almost anywhere for protection from the summer sunshine and that is not likely to be such a critical factor in tortoise survival as the protection from winter cold. This latter may be of less significance in the warmer portions of the desert, where it is not known whether they utilize such special winter dens.

From November 27, 1936 to March 2, 1946, 281 tortoises which lived on this area have been marked, including 9 which have been removed as specimens for study and 7 others from elsewhere which have been released on the area by way of experimentation.

Occasionally a new unbranded tortoise is still discovered among those branded. The proportion of branded to unbranded tortoises suggests that in round numbers, about 300 tortoises inhabit the area and make up the permanent population of the colony. This represents approximately one tortoise for each 4 acres of land—a relatively high concentration. Elsewhere the concentration of tortoises may be much lower.

The population has a very high percentage of adult individuals that show no further growth. Only a few young tortoises have been encountered. The data are inadequate to show the exact proportion, but is estimated to be less than 5%. This small percentage of increase indicates a very stable population with long-lived individuals and a very low replacement by young.

During this study, records have accumulated to show that remains of 30 dead individuals have been found, an average rate of about 3 per year or 1% of the population. This, of course, probably does not represent all the deaths, but is believed to indicate that the death rate is not very high compared with that of birds and mammals. Even if the death rate were 3 or 4 times as great, it would still be less than 5% of the population.

An accurate method of computing ages has not been developed, but measurement data indicate that growth is usually exceedingly slow after a tortoise reaches a mature length which ranges in females from about 230 to 265 mm. and in males from about 250 to 300 mm. although it may be quite rapid prior to that time. Bogert (1937:191) indicated rapid growth in specimens of 150 and 250 mm. length, but practically none in one of 287 mm.

The method of counting growth rings on the scutes is unreliable. Miller (1932:195) showed that the growth rings do not accurately indicate age. A tortoise kept by Mattie Sanford in Salt Lake City was painted in 1937 in order to watch for new growth rings. Although fed liberally and well tended, a new ring did not appear until 5 years later, in 1942. It had approximately 42 rings on the scute.

Home Range

The records and observations indicate that each tortoise has a small home range which usually covers about 10 to 100 acres and which overlaps the home ranges of other tortoises. There is no evidence to indicate that the area is divided into individual territories that are defended.

Home ranges have been obtained by plotting on the map the various points at which the tortoise has been observed at various times during the study. See Figures 22 and 23 and Table 6. Some tortoises have been captured more than others, but the general pattern is about the same in nearly all the cases. As would be expected, there are a few aberrations from the normal.

Distribution within the Colony

Of a total of 272 tortoises released prior to February 10, 1946, one tortoise has been recaptured 22 times; two 17 times; two 15 times; four 13; four 12;

four 11; three 10; five 9; seven 8; six 7; eleven 6; twenty-two 5; fifteen 4; nineteen 3; thirty-one 2; forty-seven once and 89 have not been recaptured. When plotted on a graph, they make a curve shown in Figure 24.

It is obvious when compared with a curve of calculated random distribution (Poisson distribution assuming all factors random) that this must be explained upon some basis other than chance alone. It may be explained, however, upon the basis of irregular sampling of the population. This is true because the original small central area was sampled much more thoroughly than later additions.

Study of the home ranges, indicates that each tortoise tends to remain on a given area with which it is familiar. It does not always use the same den each year, but may shift to nearby dens in its area. A tortoise does not always use the same hole con-

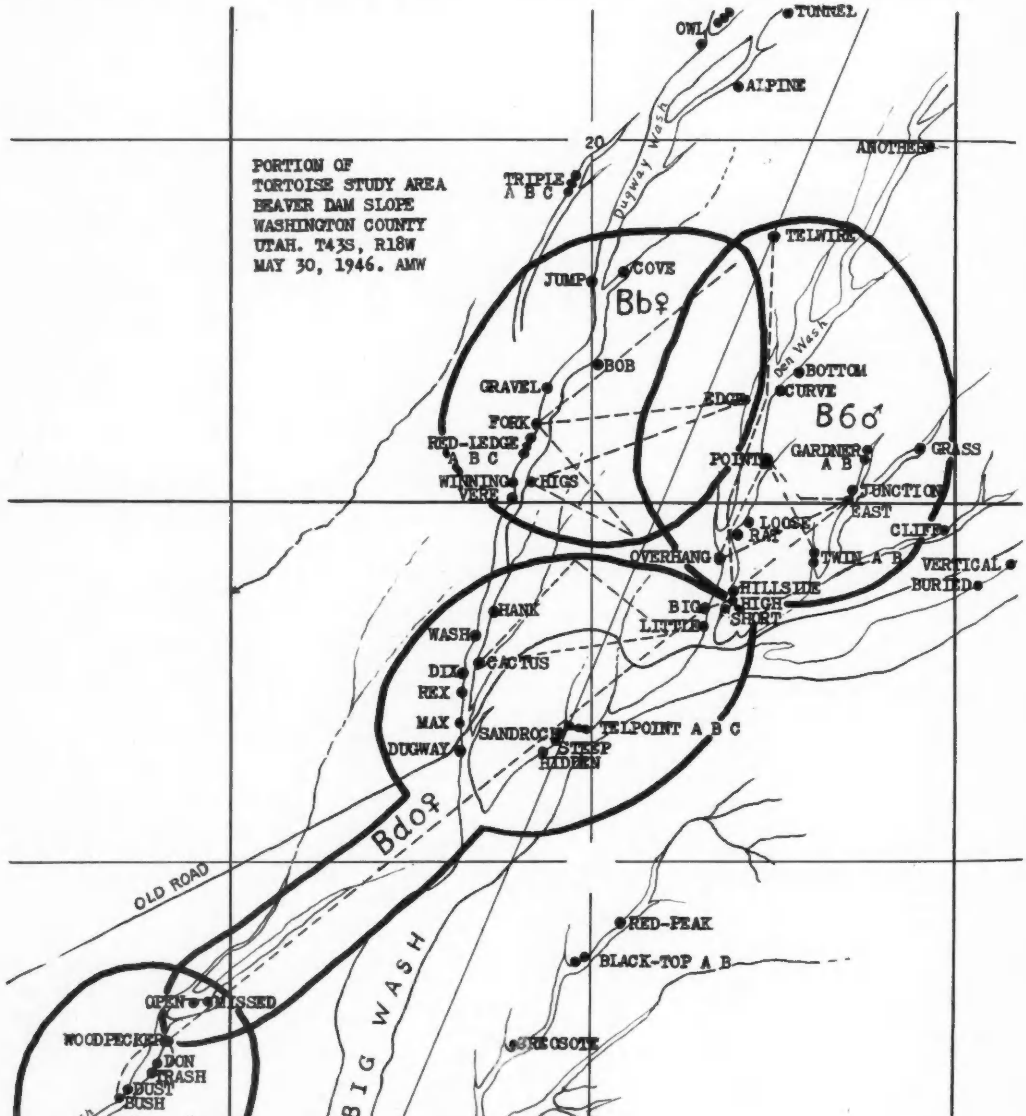


FIG. 22. Map A of home ranges, showing method of designating boundaries.

tinuously throughout the summer, but may move from time to time to other holes within its home area.

Seldom do two tortoises inhabit the summer holes simultaneously. In the few cases observed, a pair (male and female) were together. The dens are nearly always inhabited by groups which are probably feebly social in nature. The maximum number found in any one den simultaneously is seventeen.

It may be noted in the table that tortoise B7♂, Bfq♀, Bp♀ were inhabitants of dens in the lower part of Den Wash; tortoises Bl♀, Bs♂, Cl♂ and M♂ inhabited dens in the lower Dugway Wash; tortoises C♀ and Ca♀ crossed from one wash to another and occupied dens in both; tortoises Bd♀, C5♂ and ah♂ lived mostly east of Den Wash; Bf♀ wandered from Fork Den in Dugway Wash across

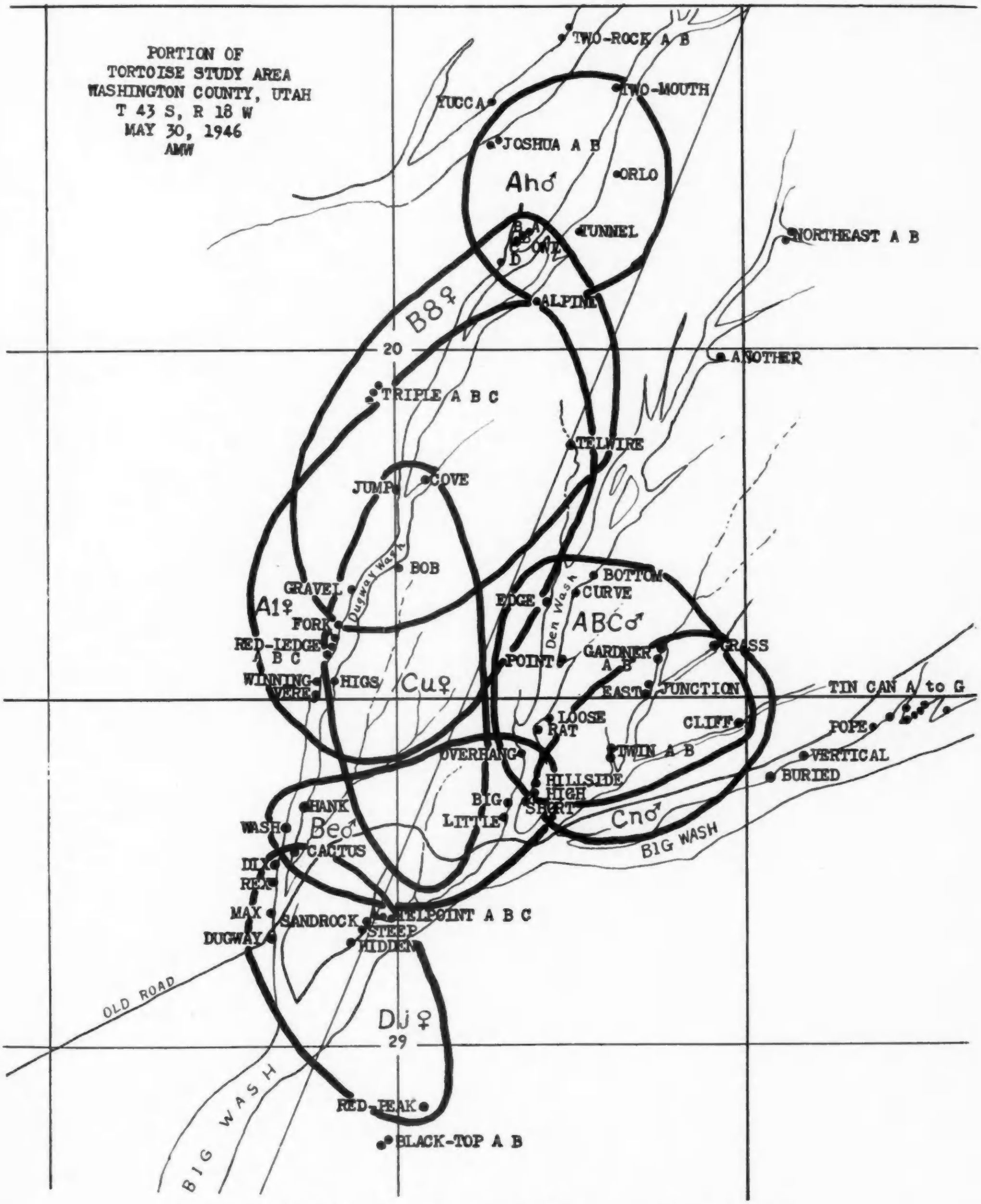
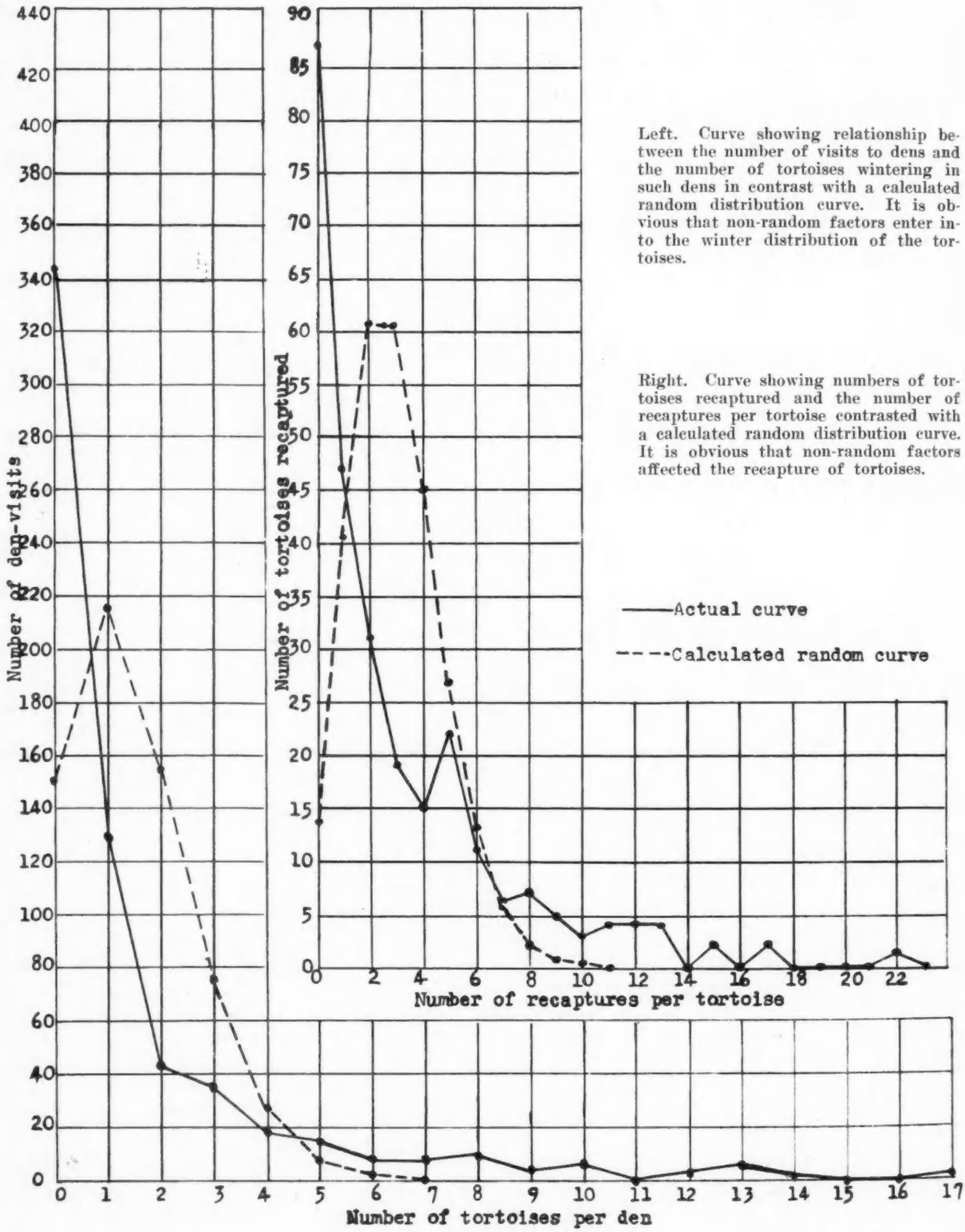


FIG. 23. Map B of home ranges, showing how they overlap one another.

Den Wash to Cliff Den near Big Wash; and tortoises Ao♂ and Ap♂ were found only in dens in Ritz Wash in the southwest corner of the area.

In Figure 22, the broken lines indicate straight lines between points of capture and the heavy circular lines enclosing an area around such points indicates an approximation of the home range. It may be noted that Bdo♀ lived around the central area for several years, then suddenly moved to the Ritz Wash area.



Left. Curve showing relationship between the number of visits to dens and the number of tortoises wintering in such dens in contrast with a calculated random distribution curve. It is obvious that non-random factors enter into the winter distribution of the tortoises.

Right. Curve showing numbers of tortoises recaptured and the number of recaptures per tortoise contrasted with a calculated random distribution curve. It is obvious that non-random factors affected the recapture of tortoises.

FIG. 24. Distribution curves.

TABLE 6. Sample Tortoise Records showing date and place of successive captures.

B7 ♂	
11-25-37	Hillside
11- 5-38	Hillside
2-18-39	Hillside
5-20-39	SW. of Little
7-14-39	W. of Big
9-30-39	Hillside
11- 4-39	Overhang
11-18-39	Short
11-24-39	Big
4- 4-40	Overhang
8-19-41	Big
3-22-42	Overhang
12-26-42	High
3-19-43	High
3- 4-44	Overhang
11-17-45	Overhang
1-27-46	Short
Bf ♀	
11-28-36	Big
5- 6-39	E. of High
7-14-39	W. of Little
7-17-39	W. of Little
9-30-39	SE. of Twin
11-18-39	Short
11-24-39	Short
2-17-40	Fork
4- 6-40	NE. of gravel
1-18-41	East
3-22-42	Edge
12-27-42	Edge
10-20-45	Cliff
Bl ♀	
7-15-39	SE. of Dugway
9-30-39	W. of Dugway
11-23-39	Dugway
2-10-40	Dugway
11- 9-40	Dugway
3- 8-41	Dugway
1-24-42	Dugway
2-13-43	Dugway
10-31-43	Dugway
1-28-45	Dugway
10-28-45	Dugway
Bd ♀	
11-28-36	Big
11-25-37	Overhang
3-25-39	Point
11- 4-39	Short
11-18-39	Short
11-24-39	Short
1-20-40	Short
1-18-41	East
3-22-42	Short
12-26-42	Hillside
2-20-44	East
10-20-45	High
2- 3-46	East
Bfq ♀	
11-28-36	Big
19-28-38	Big
11- 4-39	Short
11-18-39	Short
11-24-39	Short
1-20-40	Short
4- 4-40	Short
2- 1-41	Big
6- 1-41	SE. of Big
12-26-42	Big
11-28-43	Big
1-13-45	Big
10-20-45	Big
1-27-46	Short
Bs ♂	
7-15-39	Sandrock
7-16-39	Big Wash
7-17-39	Big Wash
11-30-40	Wash Den
9- 7-41	Rex
10- 4-41	Cactus
1-24-42	Cactus
2-13-43	Cactus
10- 2-43	Hidden
1-28-45	Cactus
10-28-45	Dugway
Bp ♀	
11-28-36	Big Den
10-28-38	Big Den
11- 5-38	Hillside
2-18-39	Hillside
3-25-39	Hillside
8- 4-39	Little
9-30-39	NW. of Overhang
11- 4-39	Short
11-18-39	Big
11-24-39	Big
1- 6-40	Overhang
1-20-40	Overhang
6-29-40	Little
10-19-40	Big
2- 1-41	Short
3-29-41	Short
4-12-41	Short
3-22-42	Short
12-26-42	Hillside
3-19-43	Hillside
9-18-43	SW. of Big
9-23-44	SW. of Big
11-17-45	Overhang
Ca ♀	
8- 3-39	SW. of ¼ Corner
8- 4-39	SW. of ¼ Corner
9-16-39	NE. of ¼ Corner
2-17-40	Higs
4- 6-40	E. of Cactus
11-30-40	Higs
3- 8-41	Higs
2-13-43	Fork
1-28-45	Higs
Ah ♂	
12-31-39	Grass
7-15-40	Near East
1-18-41	East
12-27-42	East
2-20-43	Cliff
3-19-43	Grass
2-20-44	Grass
1-19-46	Grass
Ao ♂	
2-18-39	Woodpecker
3-11-39	Woodpecker
12-30-39	Missed
2- 1-41	Don

In Figure 23, several home ranges have been plotted to show how they overlap. Apparently a tortoise tends to stay in an area with which it is familiar but occasionally one moves into a new area. The sizes of home range areas vary from about 10 to 100 acres with an average approximately 50 acres.

During the study, 657 visits have been made to 93 dens, an average of 7 visits to each den during the hibernation period. Of these, 358 visits were made to dens that were empty. In the balance of the visits, tortoises were found in dens as follows: on 129 visits, one tortoise in each den; on 42 visits, 2 tortoises; 37 visits, 3 tortoises; 19 visits, 4 tortoises; 16 visits, 5 tortoises; 8 visits, 6 tortoises; 7 visits, 7 tortoises; 11 visits, 8 tortoises; 4 visits, 9 tortoises; 7 visits, 10 tortoises; one visit 11 tortoises; 3 visits, 12 tortoises; 6 visits, 13 tortoises; 2 visits, 14 tortoises; and one visit, 17 tortoises. When plotted on a graph, these produce a curve as shown in Figure 24.

When this curve is compared with a theoretical curve of random distribution (Poisson distribution assuming all factors random), it becomes obvious that the occurrence of tortoises in dens cannot be explained on the basis of chance alone. At least three non-random factors are involved (1) the tendency to occupy a den within the home range, (2) the social tendency to aggregate by entering dens where other tortoises are already present and (3) the tendency to seek comfort by concentrating in long dens where the temperatures are higher and more stable. The average number of tortoises found in occupied dens prior to January 1, 1946 is 3.11 tortoises per den, but there may have been additional tortoises in inaccessible portions of many of the dens, which, if known, would probably have raised this average.

CONSORTISM

The digging of dens and summer holes by tortoises opens shelters in the ground which other animals use. In some cases, such use does not interfere with the tortoises, but in other cases interference doubtless does result. This brings the tortoises into intimate contact with other animals.

COMMENSALS

During the investigation, especially when opening the dens or when removing tortoises, commensal animals were encountered or evidences of their presence (remains, tracks, traces, droppings, property or work) have been observed.

One of the most conspicuous and persistent commensals is the packrat, which makes characteristic piles of rubbish containing sticks, stones, bones, bark, leaves, pieces of cactus and other small objects around its burrows. These packrat piles or "nests" are of common occurrence just inside the mouths of dens, sometimes nearly filling the passageway. On several occasions tortoises were found actually covered by such rubbish.

This packrat litter scattered along the passageways over the loose dust in the bottom of the dens furnishes a bedding ground in which certain kinds of arthropods dwell. The cone-shaped pits of the larvae of the ant-lion, Myrmelionidae, have been observed in the dust in the bottom. Larvae of certain beetles, Tenebrionidae, have been uncovered in the litter. Spider

webs of various kinds have been seen festooned in various places in the tunnels and specimens of several species have been found in the litter. Silverfish are common everywhere and occasional cockroaches are observed.

Specimens of the banded gecko have been dug out of the dens where they were hibernating. Two specimens crowded together side by side in a small hole were found in edge of Woodpecker Den on December 17, 1939. Another was found in the debris on the floor of East Den, December 30, 1939; two in the gravel in the bottom of Grass Den on December 31, 1939; and one in the dust in the bottom of Edge Den, January 6, 1940.

The desert scaly lizard, has also been found hibernating in the bottom of dens. Two were found in Dugway Den, November 23; one in East Den, December 30, 1939; one in Edge Den, one in Loose Den and one in Northeast Den, January 6, 1940; one in Hillside Den and one in Woodpecker Den, February 1, 1941. It seems curious that the common brown-shouldered lizard, has never been found hibernating in any of the dens.

Certain snakes also use the dens. A spotted night snake, was found hibernating in the dust and gravel in the bottom of Missed Den, December 30, 1939. Two sidewinder rattlesnakes were found in hibernation, one in Dugway Den, November 23, 1939 and one in Woodpecker Den February 1, 1941. Another specimen was found sunning itself in the mouth of Cliff Den, March 8, 1941.

Two Great Basin rattlesnakes have also been found in dens. One was observed November 4, 1939 emerging from a lateral hole and entering Telpoint B Den while excavation of the den was in progress. The other encounter was even more dramatic. The junior author was attempting to remove a single tortoise in the farthest end of Short Den in midsummer, July 15, 1940, when a large rattlesnake emerged into the den from a lateral hole about a foot from his hand and started toward him. Upon mutual recognition, both reversed directions suddenly.

It is probable that some birds also utilize the dens. A hard-shelled pointed egg, suspected of belonging to a burrowing owl, was found in the mouth of Rex Den, April 9, 1942. Feathers of the Gambel quail were numerous in Big Den, September 18, 1943, where they had probably been left by some predator. On one occasion, a young cactus wren separated from the family flock entered Dugway Den in an effort to escape pursuit of a collector and disappeared into its dark interior. A mummified body of a young roadrunner was found in a tortoise den near the study area.

Some mammals habitually use the dens. Many live packrats and numerous rubbish "nests" have been observed in them. These rats are permanent inhabitants which do no hibernate. On October 20, 1945, a tortoise was seen entering Twin A Den, soon after which an adult Neotoma came charging out and dashed for shelter in an old rat nest in a nearby desert almond bush.

On four different occasions, Arizona cottontail rabbits have been found using the dens. Two were caught alive, one in Pope Den, and one in Dix Den March 8, 1941. Another was seen in Buried Den on the same date and a fourth one in Big Den, March 29, 1941.

A desert jack rabbit was found using a summer hole for shelter and one was observed to enter Short Den. The kangaroo rats and the Mohave pocket-mouse have all been trapped in summer holes. A scorpion-mouse, the canyon-mouse, and the cactus-mouse have all been trapped in the area nearby.

In addition to the living animals, remains such as skull, bones, bodies, or other parts have been found in dens. These include a skull of a spotted skunk, remains of a cottontail, a jack rabbit, 2 packrats, one gopher snake, and an unidentified snake. Scats of carnivores were also found, two of which contained pieces of horny material from a tortoise.

Parasites

Certain parasites also utilize the litter-strewn dens. On November 11, 1939, it was recorded that numerous small ticks have been seen crawling in the debris of nearly all dens visited. On December 30, 1939, among other things both ticks and fleas were recorded as found in the debris raked out of the bottom of East Den. It is probable that the flea was parasitic on the packrats that inhabited the den, but the ticks are known parasites of the tortoise.

The adobe tick, *Ornithodorus turicata* (Duges), was reported (Harbinson 1937:80) taken from the desert tortoise at Thermal, California as well as from the gopher tortoise from southeastern United States. Specimens from tortoises on the Beaver Dam Slope have been checked by Dr. Albert Grundmann and found to belong to the same species. Davis (1936: 1719) indicates that this tick may be a possible vector of relapsing fever in southwestern Kansas and it must be regarded with suspicion in our area.

The field notes include numerous records of individual tortoises parasitized by the ticks. It is not always clear from the notes whether the ticks were or were not attached to the tortoise, but it is certain in many cases that they were. Ticks were most often found attached to parts of the shell where bone was exposed as a result of injury, often from branding. Sometimes, however, they were attached in sutures between scutes or on the soft skin around neck, legs or tail.

Some specific references in the field notes include: three ticks taken from a crevice by the brand on tortoise 1u♂ on September 30, 1939; tortoise Bep♀ had a tick crawling on carapace, November 4, 1939; numerous ticks were found, some fastened in cracks of carapace, November 23, 1939; the tortoises in Dugway Den had ticks firmly fastened to legs, neck and other soft parts of the body, spots of blood were noted around point of attachment, "head" sometimes left attached when tick removed, February 10, 1940; in Higs Den, tortoises had ticks attached to soft parts near neck and tail, February 17, 1940; tortoise A3♂ had ticks on soft parts about neck and legs, March 2,

1940; tortoise 1e♂ very heavily parasitized by many small ticks along edge of brand, October 19, 1940; ticks on tortoise Bg♂ between uninjured scutes n and o, October 19, 1940; tortoise F1 in Telwire Den had numerous small ticks filled with bright red blood in sutures of carapace, November 28, 1943; broke one large blood-filled tick near anus of tortoise Du♀, February 20, 1941; tortoise 1u♀ (see above) resting in shade of a Joshua tree had about 34 small ticks under sliver of bone on brand, May 27, 1944.

It seems certain from the notes that the ticks not only infest the litter of the dens, but also remain on tortoises and are carried about during the summer wanderings. It is probable that this tick also infests other animals such as snakes, lizards and mammals.

For several years, we were inclined to believe it did not attack man, but on October 20, 1945, the junior author, after crawling in several dens and handling several tortoises, discovered a small tick attached to his right forearm that had already begun to suck blood. After removal, a small red spot developed at the site of attachment. Another tick was discovered on his arm at home after a trip to the dens on November 17, 1945.

On November 18, 1939, tortoise Bep♀ was found to have fly maggots on plates B and p where it had been branded. It had recovered at the time of later recaptures. Tortoise Af♂ had swollen places under the jaw and on the side of the head and appeared to be sick on November 25, 1939, but was alive and well on April 12, 1941. Tortoise Bh♂ when handled on November 30, 1940, had a wet condition of the nostrils and about 4 drops of fluid dripped from them.

Mold has been observed growing on tortoises on two occasions. Tortoise ar♂ had yellow and white fungi growing on the shell, especially on the plastron, February 18, 1939. Tortoises Ah♂ and C2♂ both had mold growing on fresh brands, March 4, 1944. All of these were in dens where presumably humidity was relatively high.

PREDATORS

The carnivores of the area are regarded with suspicion as possible predators upon the tortoises. Attention has been focused particularly upon coyotes, cats and badgers, but foxes, skunks, ring-tailed cats and hawks are not beyond suspicion. Definite evidence comes mainly from scratches which appear to be tooth marks on living tortoises, from broken shells and from scats.

On two occasions, scats were found which contained tortoise material. One picked up in Trash Den, February 1, 1941 contained horny material from a tortoise. Another picked up on the flat near Joshua Den, December 8, 1945 contained scales and skin from soft parts of the body. These scats were assigned to coyotes.

Of the remains of 30 dead tortoises found, at least 6 offered definite evidence of having been eaten by carnivores. On January 18, 1941, Charles Retzell, a service station operator, reported seeing a bob-cat kill and eat a tortoise by a desert almond in Dugway Wash near Cactus Den. Remains of this tortoise were found, February 1, 1941 at the place designated. A piece of the front part of carapace, the head, front legs and most of the internal organs as well as the distal portions of the hind legs had all been removed.

On April 12, 1941, a six-inch tortoise was found with the anterior projection of the plastron broken off back to the bridge. The head, legs and anterior internal parts and external parts of hind legs were gone, as if eaten, whereas the posterior-internal parts that had been left in position were riddled in the pattern characteristic of blow fly larvae. On the same date, also found was a piece of a shell of a very young tortoise having only 2 or 3 growth rings, that may have been partly eaten by a carnivore. Another small tortoise, estimated at 50 or 60 mm. in length that had been about half eaten probably by a carnivore was found in a wash near Higs Den. A part of the shell of tortoise Do♀, in which the whole dorsal part of the carapace had been broken and most of the vertebrals and costals removed was found across the wash south of Buried Den, December 4, 1945. All of the internal organs, all of the hind legs and tail, the head and neck, and all of the front legs except the skin that closed the anterior opening of the shell had been eaten and the shell cleared out so clean inside that there was no indication whatever of any blow fly larval activity. In addition, there were tooth marks in 3 places around the edges of the carapace indicating unsuccessful attempts to break the shell from the edge. How a break in the dorsal part of the shell was started is not clear.

Another shell, similarly cleaned, that of tortoise A2♀, was found near Overhang Den, December 8, 1945. This shell was lying on its back with the plastron and all internal parts as well as head, legs and tail removed and thoroughly cleaned so there was nothing left for blow fly larvae. A possible suggestion of how the shell was broken open can be derived from a small hole about the size of a carnivore tooth in the anterior part of the carapace. Nearby were other tooth marks that showed the pattern of wildcat teeth. Possibly clamping the jaws on the outside of the shell may be sufficient in some cases to penetrate the shell and break out a piece. Once started, additional pieces could be broken off until access was gained to the interior.

Remains of a small tortoise about 5 inches long, which had been partly eaten was found between Alpine and Cove dens, November 30, 1940, but at that time the cause of death was not satisfactorily assigned. Suspicion that carnivores were responsible for the death attaches to several other shells that have been picked up from time to time, but since the evidence is not satisfactory, they will not be cited. Many living tortoises have been observed, in which tooth-marks have been found around the edges of the shell, indicating that they had survived the attacks of predators. Those records of damage to front legs cited under "Abnormalities Due to Injuries," probably resulted from carnivore activity.

It is interesting to note that other writers have come to similar conclusions. Camp (1916:512) remarked that "they probably fall prey in numbers to raptorial birds and mammals." Miller (1932:197) was skeptical but Klauber (1932:128) was more convinced. He reported finding shells in San Bernardino County, California and stated: "Evidently these tortoises have enemies which are able to destroy them in spite of the protection of the shell; in two instances the shells were intact, in two others crushed and scattered."

GENERAL WELFARE

The predator pressure on tortoises probably varies from time to time. Perhaps it is correlated with the rabbit cycle. Rabbits, especially cottontails, were very abundant during the years 1941 and 1942, but the cycle reached a low from 1943 to 1946. During late 1945 and early 1946, tortoise fatalities obviously due to carnivores showed an increase when compared with the few such signs observed earlier. Perhaps the tortoise is subjected to a greater amount of predator pressure, especially from bobcats and coyotes, when the usual food—rabbits—is scarce.

"The old ones are a favorite delicacy among Indians and Mexican section-hands who live with their families along the railroad lines" in Southern Califronia according to Camp (1916:512). Bailey (1928:372) said that "herein lies the greatest danger to this interesting desert dweller, for ages an important article of food."

The killing of tortoises by automobiles and trucks on roads, the commercial exploitation of tortoises by service station operators and other desert dwellers as well as the frequent removal of tortoises by passing tourists probably constitute a greater danger than does the use of tortoises as food under modern conditions. On March 9, 1946 the area in Castle Cliff Wash near Castle Cliff Station was explored. Numerous abandoned dens, without tortoise droppings or other sign of recent occupancy, were found within a radius of over one mile. The situation was much the same within a mile of Yucca Service Station on Beaver Dam Slope. Outside the orbit of each of these establishments, tortoises were found, although few in number. It seems probable that the constant removal of tortoises from an area by service station operators and others for sale to tourists is the greatest known threat to tortoise welfare.

A large patch of climbing milkweed which is known to be poisonous to livestock occurs in Big Wash a short distance southwest of Little Den. It is suspected that this plant might also be poisonous to tortoises.

Brush fires may occasionally be dangerous to these slow-moving reptiles. According to Lonnie L. Moseley, a student at Dixie Junior College, about fourteen empty tortoise shells were observed in a small portion of a burned area covering approximately two square miles about ten miles south and slightly east of Bunkerville, Nevada, physiographically a continuation of the Beaver Dam Slope, in December, 1942. The tortoises were assumed to have been burned during a fire which occurred about two years earlier.

The effect of the occasional burning of trash piled by pack rats at the mouth of winter dens is unknown, but judging by the number of dens with smoke-blackened roofs, it has occurred from time to time. Such fires that interfere with tortoise habitat may be a factor in decimation.

Loss of life in occasional floods which sweep down these washes is possible but the loss therefrom is likely very light. Tortoises in captivity have been found surprisingly helpless when they have floundered into large basins of water. One, believed to have drowned, was found floating in a large water pan in the reptile pit at Dixie Junior College in February, 1946. Perhaps a tortoise overtaken by a flood could struggle ashore, but flash floods from cloudbursts are so swift and turbulent that they would be more likely to carry a tortoise out of its home range or cause it to drown. However, such floods are of infrequent occurrence and the drain on the population from this source is probably slight.

Overgrazing and trampling of an area by sheep and other livestock doubtless causes deterioration in the tortoise habitat but does not prevent tortoise survival. The tortoises of the large colony studied have lived in an area where they have been in constant competition with livestock for food.

Regulation of human interference with tortoises, prevention of habitat destruction by fire, and reduction of predator destruction of tortoises by any possible method seem to provide the best means of insuring the survival of these most interesting members of the desert fauna.

SUMMARY

This is the report of a study of a semi-isolated colony of about 300 desert tortoises living in a small basin at the mouth of a large canyon at the west foot of the Beaver Dam Mountains in extreme southwestern Utah, near the Arizona line and about five miles from Nevada; altitude 3200 to 3500 feet.

The area studied lies in the Lower Sonoran Life Zone of Merriam in the eastern edge of the Great Basin Physiographic Province of Atwood, in the Mohavian Biotic Province of Dice (1943), the Western Desert Scrub Association of Clements (1920) and the Clistoyucca-Larrea Association of Hardy (1945).

The dominant cover consists of Joshua trees and creosote bushes but these are interspersed with cactuses, yuccas, black brush, desert almond and other bushes as well as grasses and herbs.

The climate is typical of the desert areas of the southwest: low precipitation and extremely variable temperature. It is probably similar to that of St. George which has an average annual precipitation of 8.73 inches, a growing season averaging 196 days, a mean temperature of 60.7° F., an extreme range from −11 to 116° F. and a double drouth cycle in June and November.

The fauna includes such carnivores as the bobcat, coyote, fox, badger, skunk, and ringtail; such rodents as the antelope ground squirrel, kangaroo rat, pocket

mouse, scorpion mouse, cactus mouse, canyon mouse, pack rat and pocket gopher; jack rabbit and cottontail; such birds as the Gambel quail, ladder-backed woodpecker, cactus wren, mockingbird, shrike, Scott oriole and the desert sparrow; such lizards as the banded gecko, collared lizard, leopard lizard, chuckwalla, gridiron-tailed lizard, scaly lizard, brown-shouldered lizard, desert horned lizard, and the desert whiptail; such snakes as the red racer, gopher snake, night snake, and 3 species of rattlesnake.

Studies of this colony began November 28, 1936, supplementing general studies begun in 1930, have been continued to 1946, during which time 90 trips of one to four days duration have been made to the area and 281 tortoises have been branded or otherwise marked for individual identification, many of which have been recaptured from time to time. The total recaptures number 812 and total records number 1093.

The data accumulated from recaptures have been used in computing growth, in plotting home ranges, in studying distribution, behavior patterns, life history and adaptations. Individual specimens have been studied and three males and three females have been dissected.

The typical shell contains 37 scutes on the carapace and 16 on the plastron in addition to some small axillary and inguinal plates, but there are many variations of 1 to 4 scutes in either direction. The bones of the shell underlying the scutes usually number 50 in the carapace and 9 in the plastron, differing from the scutes in form, size and arrangement. The ratio of height to length averages about .42 and that of width to length about .74.

The scutes of the carapace include a central row of 5 vertebrals, two rows of 4 costals, all surrounded by two rows of 11 marginals that are separated by a nuchal and a pygal. The plastron contains 6 pairs of paired scutes. The bones of the typical carapace include dorsally a central row containing one nuchal, 8 neurals, 2 suprapygals and one pygal; a dorsolateral row of 8 costals on each side; and a lateral row of 11 peripherals along each edge. The plastron contains one single bone and 4 pairs of bones. Neural spines of certain vertebrae and the ribs fuse with certain neural and costal bones (see "Skeleton"). As usual in tortoises, the pectoral and pelvic girdles are set inside the shell.

It was discovered that both branding and natural injuries to the shell initiated a very slow sequence of shell repair in which a piece of scute is shed exposing bone and a new part of the scute is formed under the bone which is in turn shed and allows the new part to grow up into place on the surface with a new piece of bone underneath. This appears to indicate that both the scute and underlying bone are dermal in origin. In general, it takes about 3 or 4 years to shed the injured part of the scute and expose the bone and about that much longer to shed the bone and finish the regeneration.

The internal systems are quite typical of turtles in general but there are minor deviations from the general pattern. The ventricle of the heart is triangular in shape and is connected with the auricles by a narrow constriction and the arterial trunk from the ventricle is not attached to the auricles. The pancreas appears to consist of a long slender lobe. A large gall bladder is present.

Beyond the stomach, the small intestine makes a loop around the right side and returns to a point near the center of the coelom where it abruptly enlarges into a very conspicuous large intestine that crosses the coelom three times and then gradually reduces in size so that the last half of the large intestine is intermediate in size. This large central portion holds much food for long periods of time. During hibernation, it appears to be always full, with little, if any, digestion taking place. It appears to contain nemas at all times. All pellets tested by Dr. Margaret Schell have yielded nema eggs. How the young become infested has not been determined.

The rounded flattened reddish brown kidneys lying behind the peritoneum connect by means of a short ureter to the neck of the large bilobed urinary bladder which usually contains much liquid and large quantities of solid particles of uric acid. This is seldom voided and large quantities of the waste can be stored for long periods without losing water. The accessory bladders described for other turtles are reduced to small pouches.

In three cases dissected, the left ovary was much better developed than the right, having 3, 5 or 7 large yellow eggs against one or none. The uteri appear to be joined externally but have separate sphincters internally. The males have the two halves of the penis lying side by side in the ventral part of the cloaca forming a urethral groove between them. The two are joined together posteriorly by the glans. Anteriorly they are bent and bulge the cloacal wall into the coelom when at rest. When excited they enlarge and straighten thrusting the penis out the cloaca. The testes transmit their products through a much coiled epididymus which empties into the anterior end of the urethral groove.

The sexes can usually be distinguished by four characters which become more manifest in adult males: the gular prong is longer and more upturned, the inguinal depression is usually deeper, the tail longer, and size larger but there are some intermediates that are difficult to place properly.

It was found that the tortoises have behavior patterns that are geared to both daily and seasonal cycles which are adapted primarily to seeking comfortable temperatures and conserving moisture. The seeking of food and mates occurs only when temperature and moisture conditions are near optimum.

Tortoises, like other cold-blood (ectothermic) animals tend to take their body temperature from the environment, mainly from the soil on which the body rests, but also from sunshine and air. The surface soil usually provides optimum temperatures during the warm days of spring and fall and the cool nights of summer. Lethal conditions occur during the torrid summer and the cold winter. Uncomfortable

conditions occur between the optima and the extremes.

These tortoises instinctively find the most optimal conditions available. This behavior tends to take them into comfortable situations so that they avoid and do not actually encounter the uncomfortable and lethal conditions that come to the place from which they move.

The annual behavior pattern leads them in the winter time into underground dens which are long horizontal tunnels in the banks of washes. Beyond 15 feet, nearly uniform temperatures devoid of daily fluctuations exist. After about six months underground, this pattern takes them out of the dens onto the surface for the summer.

Here the daily pattern modifies the seasonal pattern. If the nights are too cold or the days too hot for comfort, the tortoise goes underground again, but in a different place. For this purpose, a tortoise digs an individual hole about 3 or 4 feet in length sloping downward at about a 30° angle where it finds comparative comfort while conditions are uncomfortable or lethal on the surface.

While the seasonal and daily behavior patterns have been described in terms of temperature, they can also be described in terms of moisture comfort. There is little or no opportunity for the tortoise to drink water and it must depend upon the water obtained in its food to supply its needs. The supply comes mainly from the succulent vegetation of spring and fall. This is the chief source of food from which fat is stored for use in estivation and hibernation. The fat yields more metabolic water than the weight of the fat that is burned. The surface of the body is waterproofed by keratin. The nitrogenous wastes are stored mainly as insoluble uric acid in a bladder containing water where it may be kept for weeks or months without discharge.

The main loss of moisture comes from breathing. This loss becomes excessive in hot dry weather. If a tortoise moves into its summer hole to avoid hot weather, it also avoids excessive loss of moisture.

Other adaptations are concerned with activity. In appearance, it is very awkward but has remarkable agility on rocky hillsides and is able to climb unexpectedly steep places. Such agility is also displayed when it is turned upside down on its back. It is then able to right itself in most cases, but if left too long in such a plight, it would be liable to suffocation from the weight of intestines on its lungs.

When legs, head and tail are withdrawn into the shell, it offers a formidable passive resistance defense against natural enemies, but even so, some carnivores are able to penetrate its defense and prey upon it. Within a den, some tortoises show a form of active resistance to being removed.

The 300 tortoises of the colony, occupying about 1200 acres of land are so distributed that each tortoise has a small home range which more or less overlaps that of others. There is no evidence available to indicate that either home range, den or summer hole is defended against others. On the contrary, evidence is presented which shows that there is a feebly social tendency for tortoises to enter dens together and form winter aggregations.

A review of the life history indicates that 3 to 7 eggs are laid in holes in the ground probably in the mouths of burrows in early summer. Hatching usually occurs in the fall. A well-developed fetus from an unhatched egg is described, which shows that the shell containing scutes without growth rings had a yolk sac attached to the posterior middle of the plastron which was incomplete at that point and bulged outward to meet the yolk sac.

At time of hatching, an egg tooth is present, a small yolk sac is still visible and there is a general wrinkling of the plastron around it as well as a large wrinkle across the plastron from bridge to bridge, all of which straighten out slowly in a few months.

Young tortoises grow slowly, reaching a length of about 100 mm. in 5 years, at which time the flexible shell of the young gradually becomes hardened like that of an adult. Sexual maturity is estimated to be reached between 12 and 20 years of age, but the total life span, although long, is for lack of evidence not estimated.

It is believed that adults slow down in rate of growth as maturity is reached and probably become approximately stable in size. Adult males range in length from about 250 to 316 mm. and females about 230 to 265 mm.

The courtship procedure is not well understood. However, the males sometimes approach other tortoises with necks outstretched and head bobbing up and down. This may or may not be reciprocated. At courting time, the males are usually aggressive, often biting at front legs or edge of shell of a non-resisting tortoise, whether male or female. If the recipient of the attention turns away, the male will often attempt to follow and a series of circlings, one around the other results.

This usually leads to attempts at coition but in the laboratory, completion has not been observed. In the attempt, the male stands with front feet resting on the other's carapace with the inguinal depression against the other's caudal scute and makes a bobbing motion attempting to make contact while the head is hooked over the end of the gular prong.

The winter dens provide shelter which many other animals utilize as commensals. These include such arthropods as ant lion, tenebrionid beetles, silverfish, spiders and ticks; such reptiles as banded gecko, desert scally lizard, and rattlesnakes; such birds as burrowing owl, roadrunner and quails; such mammals as pack rats, cottontail rabbits, kangaroo rats, mice and possibly some kinds of carnivores.

The parasitic adobe tick has been observed both in the dens and attached to the tortoises. Elsewhere, it is known to be a vector of relapsing fever and may prove to be so here.

The life span is so long and the rate of reproduction so low that there is grave danger of extermination in areas where there are heavy inroads upon the population. It is in dire need of protection from the type of commercialism represented by service station operators gathering them for the tourist traffic.

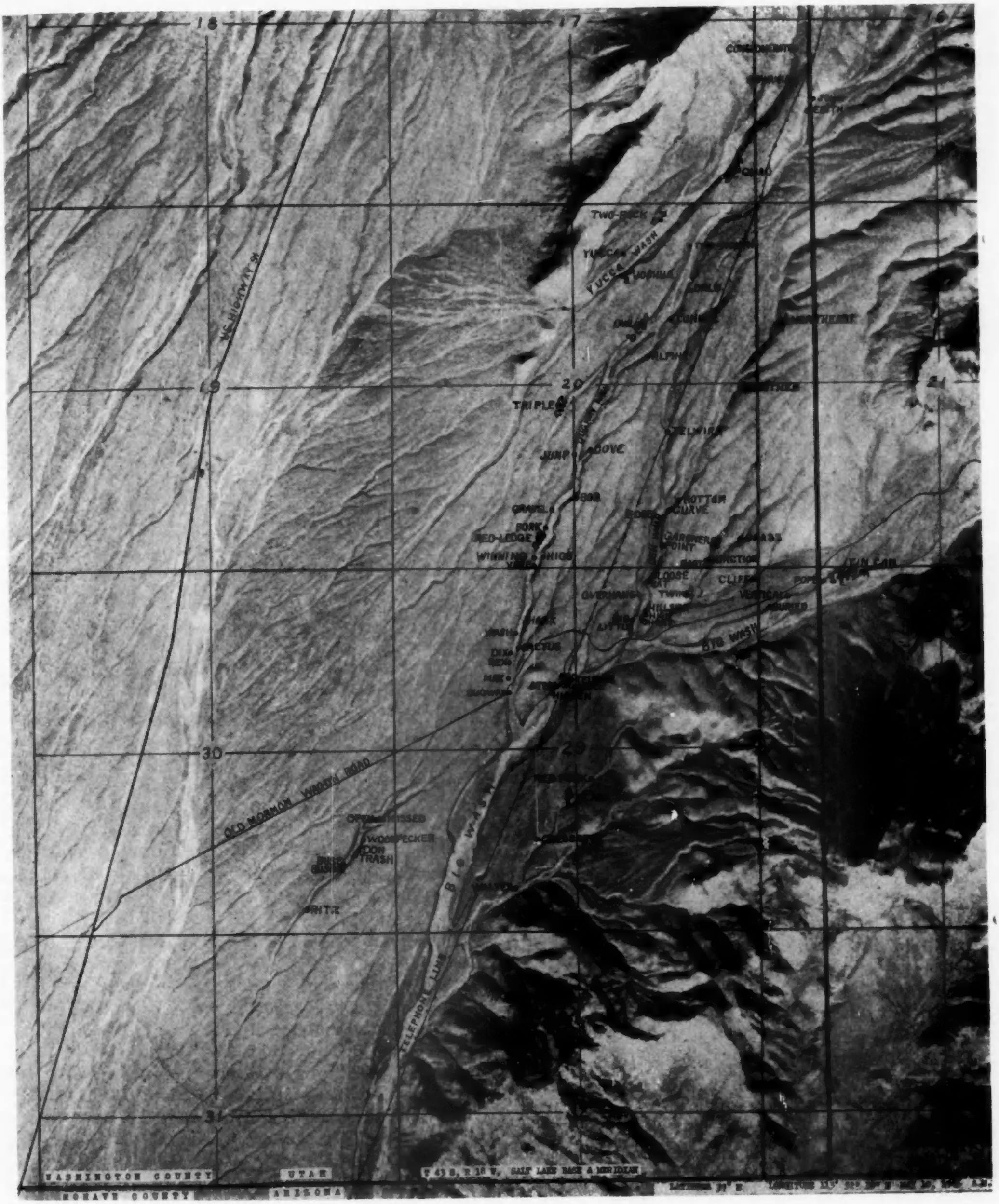


FIG. 25. Map of tortoise study area, Beaver Dam Slope, Utah

BIBLIOGRAPHY

Allen, Morrow J. 1932. A survey of the amphibians and reptiles of Harrison County, Mississippi. Am. Mus. Novit. **542:** 1-20.

Alter, J. Cecil. 1941. Supplementary climatic notes for Utah. In Climate and Man. U. S. Dept. Agr. Yrbk. (1941) 1157-1158.

Anonymous. 1941. Keeping cool. Lancet **241:** 77-78.

Atwood, Wallace W. 1940. The physiographic provinces of North America. N. Y. 1-536.

Babcock, S. M. 1912. Metabolic water: its production and role in vital phenomena. Wis. Agr. Exp. Sta. Res. Bull. **22:** 87-181.

Bailey, Vernon. 1923. Sources of water supply for desert animals. Sci. Mo. **17:** 66-86.

1928. The desert tortoise, an example of unusual adaptation. Nature Mag. (1928) 372-374.

Baldwin, Ernest. 1940. An introduction to comparative biochemistry. Cambridge, England: 1-110.

Behle, William H. 1943. Birds of the Pine Valley Mountain Region, southwestern Utah. Bull. Univ. Utah **34:** 1-85, 13 figs.

Belehradek, J. 1935. Temperature and living matter. Protoplasma Monagraphien, **8:** 1-277.

Benedict, F. G. 1932. The physiology of large reptiles. Publ. Carnegie Inst., Wash. **425:** 1-539.

Bogert, Charles M. 1930. Annotated list of the amphibians and reptiles of Los Angeles County. Calif. Bull. So. Calif. Acad. Sci. **29:** 1-14.

1937. Note on the growth rate of the desert tortoise, Gopherus agassizii. Copeia (1937) 191-192.

1939. Reptiles under the sun. Nat. Hist. **44:** 26-37.

Bogert, Charles M. and James A. Oliver. 1945. A preliminary analysis of the herpetofauna of Sonora. Bull. Amer. Mus. Nat. Hist. **83:** 303-425.

Borradaile, L. A. 1923. The animal and its environment. London 1-399.

Boulenger, G. A. 1889. Catalog of chelonians in the British Museum. London.

Buxton, P. A. 1923. Animal life in deserts. London 1-176.

Cagle, Fred R. 1937. Egg-laying habits of the slider turtle (Pseudemys troostii), the painted turtle (Chrysemys picta), and the musk turtle (Sternotherus odoratus). Jour. Tenn. Acad. Sci., **12:** 87-95.

1942. Herpetological fauna of Jackson and Union counties, Illinois. Amer. Mid. Nat. **28:** 164-200. (p. 196).

1944. Sexual maturity in the female of the turtle, Pseudemys scripta elegans. Copeia (1944) 149-152.

1944. Home range, homing behavior, and migration in turtles. Misc. Publs. Mus. Zool., U. of Mich. **61:** 1-34, 2 pls.

1945. Recovery from serious injury in the painted turtle. Copeia (1945) 45.

Camp, C. L. 1916. Notes on local distribution and habits of amphibians and reptiles of southeastern California in the vicinity of Turtle Mountains. Univ. Calif. Publ. Zool. **12** (17): 503-544.

Cassell, Richard L. 1945. The ways of a desert tortoise. Desert Magazine Dec.: 25.

Chace, Lynnwood. 1945. Fertile turtle. Nat. Hist. **54:** 418-421.

Clements, F. E. 1920. Plant indicators; the relation of plant communities to process and practice. Carneg. Inst. Wash. Publs. **290:** 1-388.

Cole, Lamont C. 1943. Experiments on toleration of high temperature in lizards with reference to adaptive coloration. Ecology **24:** 94-108.

Conant, Roger. 1938. On the seasonal occurrence of reptiles in Lucas County, Ohio. Herpetologica **1:** 137-144.

1945. In pursuit of the turtle. Fauna **7:** 34-43.

Cooper, J. G. 1863. Description of Xerobates agassizii. Proc. Calif. Acad. Sci. **2:** 120.

1870. The fauna of California and its geographic distribution. Proc. Calif. Acad. Sci. **4:** 61-81.

Corti, U. A. 1941. Zur analyse des Biotop-Bergriffes. Arch. Suisses Ornithol. **1:** 544-599 Biol. Abst. (1943) 17885.

Cowles, R. B. 1920. A list and some notes on the lizards and snakes represented in the Pomona College Museum. Journ. Entomol. & Zool., Pomona College **12:** 63.

1939. Possible implications of reptilian thermal tolerance. Science **90:** 465-466.

1941. Observations on the winter activities of desert reptiles. Ecology **22:** 125-140.

Cowles, Raymond B., & Charles M. Bogert. 1936. The herpetology of the Boulder Dam Region (Nev., Ariz., Utah). Herpet. **1:** 33-42.

1944. A preliminary study of the thermal requirements of desert reptiles. Bull. Amer. Mus. Nat. Hist. **83:** 263-296.

Cox, E. T. 1881. Notes on the tortoises of Tucson. Am. Nat. **15:** 1003.

Davis, Gordon E. 1936. Ornithodoras turicata. The possible vector of relapsing fever in southwestern Kansas. Pub. Health Repts. **51:** 1719.

Dice, Lee R. 1939. The Sonoran Biotic Province. Ecology **20:** 118-129.

1943. Biotic Provinces of North America. Univ. Mich. Press, Ann Arbor 1-78.

Dill, D. B. 1938. Life, heat, and altitude. Cambridge 1-211.

Ditmars, Raymond L. 1907. The reptiles of North America. N.Y. 1-465. Rev. ed. 1936.

Gardner, Louis S. 1941. The Hurricane fault in southwestern Utah and northwestern Arizona. Am. Jour. Sci. **239:** 241-260.

Gloyd, Howard K. 1937. A herpetological consideration of faunal areas in southern Arizona. Bull. Chicago Acad. Sci. **5:** 77-136.

Goin, Coleman J., & C. C. Goff. 1941. Notes on the growth rate of the gopher turtle, Gopherus polyphemus. Herpet. **2:** 66-68.

Grant, Chapman. 1936. The southwestern desert tortoise, Gopherus agassizii. Zoologica **21:** 225-229. N. Y. Zool. Soc.

1936a. An extraordinary tortoise shell. Copeia (1936) 231-232.

1937. Orthogenetic variation. Proc. Ind. Acad. of Science **46:** 240-245.

1937a. The "midventral keel" in Testudinata. Proc. Ind. Acad. Sci. **46:** 246-252.

1944. Symmetry and asymmetry of the medium sutures in reptilian scutellation. Herpet. **2:** 114-117.

1946. Data and field notes on the desert tortoise. Trans. San Diego Soc. Nat. Hist. **10:** 399-402.

Grinnell, Joseph, & C. L. Camp. 1917. A distributional list of the amphibians and reptiles of California. Univ. Calif. Publ. Zool. **17:** 127-208.

Gunn, D. L. 1942. Body temperature in poikilothermal animals. Biol. Rev., Cambridge **17:** 293-314.

Hallinan, Thomas. 1923. Observation made in Duval County, Northern Florida on the gopher tortoise (Gopherus polyphemus). Copeia **115:** 11-20.

Harbinson, Charles F. 1937. The adobe tick on Gopherus agassizii. Herpetol. **1:** 80.

Hardy, Ross. 1945. The influence of types of soil upon the local distribution of some mammals in southwestern Utah. Ecol. Monogr. **15:** 71-108.

Hardy, Ross, & Harold Higgins. 1940. An annotated check-list of the birds of Washington County, Utah. Proc. Ut. Acad. Sci., Arts and Lett. **17:** 95-111.

Hartweg, Norman. 1944. Spring emergence of painted turtle hatchlings. Copeia (1944) 20-22.

Hay, O. P. 1908. The fossil turtles of North America. Carneg. Inst. Publ. Washington, D. C. **75:** 1-568.

Hibbard, Claude W. 1944. A new land tortoise, Testudo riggsi from the middle Pliocene of Seward County, Kansas. Univ. Kans. Sci. Bull. **30:** 71-76.

Hitchcock, A. S. 1935. Manual of the grasses of the United States. U. S. Dept. Agr. Misc. Publ. **200:** 1-1040.

Hunter, W. S. 1942. The nature of instinct and its modification. Psychosomat. Med. **4:** 166-170. Biol. Abst. 1942: 579.

Hyman, Libbie H. 1942. Comparative Vertebrate Anatomy. Chicago 1-544.

Jaeger, Edmund C. 1922. Denizens of the desert. Cambridge 1-299.

Klauber, L. M. 1930. A list of the amphibians and reptiles of San Diego County, California. Bull. Zool. Soc. San Diego **5:** 1-8.

1932. Amphibians and reptiles observed enroute to Hoover Dam. Copeia (1932) 118-128.

1934. Annotated list of the amphibians and reptiles of the southern border of California. Bull. Zool. Soc. San Diego **11:** 1-28.

MacCoy, Clinton V. 1932. Herpetological notes from Tucson, Arizona. Occ. Papers Boston Soc. Nat. Hist. **6:** 11-24.

MacDougal, D. T. 1908. Botanical features of North American deserts. Carneg. Inst. Publ. Washington. **99:** 1-111.

McLain, R. B. 1899. Critical notes on a collection of reptiles from the western coast of the United States. T. c. p. 2. Zool. Record, 1900, Reptiles, p. 7. Contributions to Neotropical Herpetology, 1899, 8 vols.

Meek, S. E. 1905. An annotated list of a collection of reptiles from southern California and northern Lower California. Field Mus. Zool. **7:** 3.

Miller, Loye. 1932. Notes on the desert tortoise (Testudo agassizii). Trans. San Diego Soc. Nat. Hist. **7:** 187-208.

Moore, John A. 1940. Stenothermy and eurythermy of animals in relation to habitat. Amer. Nat., **74:** 188-192.

Mosauer, Walter. 1936. The toleration of solar heat in desert reptiles. Ecol. **17:** 56-66.

Netting, M. Graham. 1936. Hibernation and migration of the spotted turtle, Clemmys guttata (Schneider). Copeia (1936) 112.

Noble, G. K., & A. M. Breslau. 1938. The senses involved in the migration of young fresh-water turtles after hatching. Jour. Comp. Psych., **25:** 175-193.

Ortenburger, A. I., & R. D. 1927. Field observations on some amphibians and reptiles of Pima County, Arizona. Proc. Oklahoma Acad. Sci. **6:** 101-121.

Pearse, A. S. 1923. The growth of the painted turtle. Biol. Bull. **45:** 145-148.

Penn, Geo. H., & Karl E. Pottharst. 1940. The reproduction and dormancy of Terrapene major in New Orleans. Herpetologica **2:** 25-29.

Pickwell, Gayle. 1939. Deserts. New York 1-174.

Pope, Clifford H. 1939. Turtles of the United States and Canada. New York 1-337.

Rahn, Hermann. 1942. The reproductive cycle of the prairie rattlesnake. Copeia (1942) 233-240.

Richardson, Frank. 1945. Nevada: studies habits of tortoise. Desert Magazine April: 30.

Risley, Paul L. 1929. Anatomical differences in the sexes of the musk turtle, Sternotherus odoratus. Mich. Acad. Sci., Arts, & Lett. **11:** 445-464.

Ruckes, Herbert. 1937. The lateral arcades of certain emydids and testudinids. Herpet. **1:** 97-103.

Russell, E. S. 1941. Biological adaptedness and specialization of instinctive behavior. Nature **147:** 729-734. Biol. Abst. 1942: 17482.

Shreve, Forrest. 1934. The problems of the desert. Sci. Mon. **38:** 199-209.

Siebenrock, F. 1909. Synopsis der resenten Schildkroten, mit Bereeksichtigung der in historischer zeit ausgestorbenen Arten. Zool. Jahrb., suppl. **10** (3): 517.

Smith, Alfred. 1929. Daily and seasonal air and soil temperatures at Davis, California. Hilgardia **4:** 77-112.

1932. Seasonal subsoil temperature variations. Jour. Agr. Res. **44:** 421-428.

Smith, Hobart M. 1945. Calcified cartilage in reptiles. Herpet. **3:** 31.

Stebbins, Robert C. 1944. Some aspects of the ecology of the Iguanid genus Uma. Ecol. Monogr., **14:** 311-332.

Stejneger, Leonhard. 1893. Annotated list of the reptiles and batrachians collected by the Death Valley Expedition in 1891, with descriptions of new species. No. Amer. Fauna **7:** 159-228.

Storer, Tracy I. 1930. Notes on the range and life history of the Pacific fresh-water turtle, Clemmys marmorata. U. C. Publs. Zool. **32:** 429-441.

Sumner, F. B. 1925. Some biological problems of our southwestern deserts. Ecol. **6:** 352-371.

Tanner, Vasco M. 1928. Distributional list of Amphibians and Reptiles of Utah. Copeia **163:** 54-58.

Taylor, Edward H. 1933. Observations on the courtship of turtles. Univ. Kans. Sci. Bull. **21:** 269-271.

Terron, C. C. 1921. Datos para una Monografia de las Fauna Erpetologica de la Peninsula de la Baja California. Mem. y. Rev. Soc. Cient. "Antonio Alzate," Mexico **39:** 165.

Tidestrom, Ivar. 1925. Flora of Utah and Nevada. Contrib. U. S. Nat. Herb. **25:** 1-665.

True, F. W. 1882. On the North American land tortoises of the genus Xerobates. Proc. U. S. Nat. Mus. **4:** 434-449.

U. S. Department of Agriculture. 1941. Climate and Man. Yearbook. Supplementary climatic notes for Utah, by J. Cecil Alter (1941) 1157-1158.

Van Denburgh, John. 1897. The reptiles of the Pacific coast and the Great Basin. Occ. Pap. Calif. Acad. Sci. **5:** 35.

1922. The reptiles of western North America. Occ. Pap. Calif. Acad. Sci., 2 vols.: 1-1028.

Van Denburgh, John, & Joseph R. Slevin. 1913. A list of the amphibians and reptiles of Arizona, with notes on the species in the collection of the Academy. Proc. Calif. Acad. Sci., **3:** 391-454.

Vorhies, Charles T. 1945. Water requirements of desert animals in the southwest. Univ. of Ariz. Tech. Bull. **107:** 485-525.

Woodbury, Angus M. 1931. The reptiles of Utah. Bull. Univ. Ut. **21:** 1-129.

1933. Biotic relationships of Zion Canyon, Utah with special reference to succession. Ecol. Monogr. **3:** 147-245.

Woodbury, A. M., & Ross Hardy. 1940. The dens and behavior of the desert tortoise. Science **92:** 529 (2397).

Woodbury, Marian, & A. M. Woodbury. 1945. Life history studies of the Sagebrush Lizard Sceloporus g. graciosus with special reference to cycles in reproduction. Herpetol. **2:** 175-196.

Yarrow, H. C. 1883. Check-list of North American reptilia and batrachia with catalogue of specimens in National Museum. Smithsonian Misc. Coll. **24** (496): 1-249.

THE ECOLOGY AND MANAGEMENT OF THE PRAIRIE SPOTTED SKUNK IN IOWA

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THE ECOLOGY AND MANAGEMENT OF THE PRAIRIE SPOTTED SKUNK IN IOWA

INTRODUCTION

The prairie spotted skunk (*Spilogale interrupta* Rafinesque) is distributed throughout Iowa, and it is especially numerous in the southern part of the state. Because it is one of the more common mustelids in the state and because of its propensity for living in and about farm yards many questions arise concerning its worth and management. The Iowa Copperative Wildlife Research Unit took this problem under consideration in 1936.

The investigation was conducted on a research-management area of 17.5 square miles in the southeast corner of the state. It covered a period from March, 1939, to June, 1942, in which 24 months were spent in continuous residence on the the area. Numerous trips were made to the area while the author was in residence at Iowa State College.

Because of a dearth of basic information concerning the habits of this animal, the earlier phases of the investigation were largely concerned with a study of food habits (Crabb 1941). While the food habits were always considered, the latter half of the investigation was largely devoted to the development of a technique for trapping and handling spotted skunks (Crabb 1941a) and investigating various phases of their life history, local range, mobility, territory, general ecology and management.

There is a paucity of literature directly related to the spotted skunk, largely because it has little market value as fur, and in Iowa because it is a southern species that only recently extended its range over the state (Scott 1937). Furthermore scientists have shunned work on the species for quite obvious reasons.

I wish to express my appreciation to Dr. Geo. O. Hendrickson, major professor, and to Dr. Thomas G. Scott, Leader of the Iowa Cooperative Wildlife Research Unit, for council and encouragement during the course of this investigation. I am also grateful to Dr. Paul L. Errington for helpful advise during the composition of this paper and for criticizing the original copy. To Dr. Carl J. Drake, head of the department, sincere gratitude is felt for his keen appreciation of wildlife problems and his encouragement throughout the work. George L. Wiseman, technician employed to run the traps, is also to be commended for faithful service. To many farmers and towns people at Stockport are due a debt of thanks.

THE STOCKPORT SKUNK RESEARCH MANAGEMENT AREA

As is true of all southeastern Iowa the Stockport area was once covered by a great glacier. The residual glacial material, from 50 to 100 feet in depth, is known as the Kansas drift. The glacial drift is composed of two clays: a lower blue clay and an upper yellow clay (Stevenson 1918). The lower blue clay has been used extensively in the manufacture of drainage tiles with which much of the upland has been made arable.

On top of the glacial drift is a deposit of loess, two to three feet deep, which characterizes the Stockport skunk area in the northeast corner of Van Buren County. The skunk area comprises 17.5 square miles or about 11,200 acres. Of the 17.5 sections approximately 10 square miles are level upland almost 100% tiled and subjected to cultivation. The other 7.5 square miles have been exposed to varying degrees of erosion characteristic of the low Des Moines and Skunk River Valleys. The southwest half of the areas is drained into the Des Moines River eight miles away and the northeast corner drains into the Skunk River twelve miles to the northeast (Fig. 1).

The bulk of the upland loess soil is Grundy silt loam with a streak of Grundy clay loam of about 2,000 acres through the center. The Grundy clay loam is the most valuable soil in the county. Farm land on this soil sold in 1941 from $110 to $150 per acre. The heavily eroded southwest part of the area has been in the past and still is in many places densely wooded—a characteristic of the Des Moines River valley.

Pasturing and heavy cutting for railroad ties, mine timber, and posts have been very destructive to the more valuable woody growths. Today the woodland is largely hickory sprouts and oak stumps. The wooded area is interspersed with farms and clearings on the higher ground.

There are two important upland timber types: white oak and the white oak—black oak—red oak type. The white oak is the predominant type. The important associates include: hickories (Carya), black cherry (Prunus), black walnut (Juglans), American elm (Ulmus), and hophornbeam (Ostrya).

Shrubs characteristic of the woodland of this region are: sumac (Rhus), rose (Rosa), coral-berry (Symphoricarpos), dogwood (Cornus), hazelnut (Corylus), currant (Ribes), raspberry (Rubus), service berry (Amelanchier), virgin's bower (Clematis), hawthorn (Crataegus), St. John's wort (Hypericum), Virginia creeper (Psedera), elderberry (Sambucus), green brier (Smilax), grape (Vitis), and prickly ash (Xanthoxylum) (Geneaux & Kuenzel 1939).

The woodland pasture part of the area is of little consequence as a habitat for spotted skunks but in order to obtain a better understanding of the ecologi-

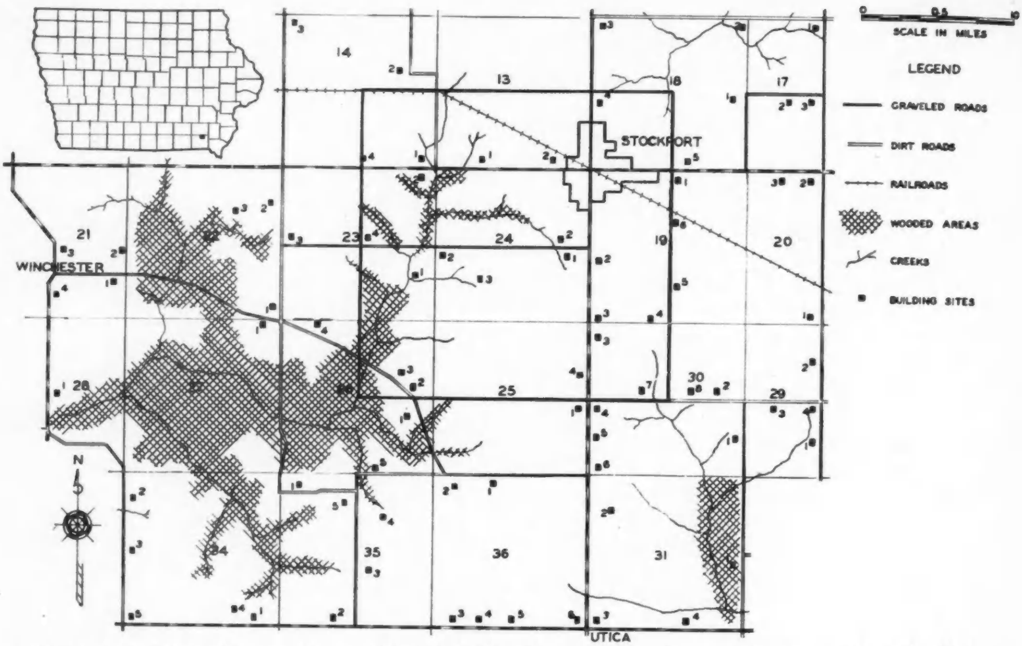

FIG. 1. Spotted skunk research area, Stockport, Van Buren County, Iowa. The area outlined in black was trapped by the quadrat system.

cal requirements of the species a diversified terrain was selected (Fig. 2).

The upland, which comprises the bulk of the Stockport skunk area, is typical of the best southeast Iowa farm land where erosion has not had its effects. It formerly supported a tall grass prairie with the typical prairie grasses such as big blue stem (*Andropogan furcatus*), Indian grass (*Sorghastrum nutans*), slough grass (*Spartina* sp.) and others. Only relics of this formation remain along fence rows and waste corners to witness its former dominance. Today this flat land is subjected to intensive cultivation, and individual farmers rely upon woodland pastures sometimes several miles from their farm site. The flat land is too valuable for much permanent pasture or many farm groves while woodland pasture is abundant and low priced.

The open level cultivated farm land provides the most favorable habitat for spotted skunks. On this part of the area the bulk of the investigation was conducted (Fig. 3).

Land utilization on four sections trapped by the quadrat method, revealed by a check in January, 1942, is shown in Figure 4.

The results of this winter check, however, are not the same as a similar check would yield during the growing season, or at any other time of the year. During the spring, as an example, as soon as the frost is out of the ground, farmers plow, disk and

FIG. 2. A spring view of uncut woodland pasture in section 23.

FIG. 3. A view to the northwest from the road on the east side of section 24.

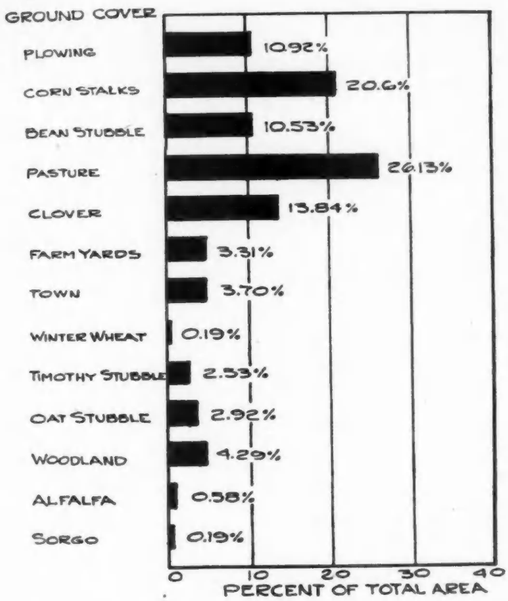

FIG. 4. Field utilization and ground conditions on four sections, January, 1942.

harrow their fields. Large areas then are bare ground. By early May the small grain covers about one-half the bare area and by the last of June soy beans, corn and other cultivated crops cover the rest.

Since the ranges of the animals and the population density figures were worked out on the four-section area during winter and spring the above tabulation of cover and ground conditions serve best to describe the area (Fig. 4, Table 1). One figure is misleading as an indicator of agricultural practice. Pasture is a much larger part of the farm land during winter than at other times of the year. Timothy, sudan grass, and brome grass, as well as the perennial bluegrass pastures, are classed under this heading at this season for they are grazed. During other times of the year much of this land would have been producing hay crops and quite a lot of it comes up after small grain for the year is harvested. Plowing is usually about one-half small grain stubble and one-half clover hay fields; consequently small grain appears considerably less important that it actually is on the area.

On the northeast corner of the area the town of Stockport is located. The population at the 1940 census was 338. The incorporated area of the town covers one square mile but less than one-fourth of this is occupied by buildings and streets. Convenient roads cross and bound the area so that every section is accessible by automobile from at least two sides. A gravel road crosses the area from north to south and bounds the area on three sides.

There are 78 farmers and sets of farm buildings on the area. The farms average 145 acres but the

TABLE 1. Land Utilization winter 1941-'42 on 2,560 acres of the Stockport Skunk Area.

Land Use	Sec. 13 Acres	Sec. 30 Acres	Sec. 26 Acres	Sec. 18 Acres	Sec. 14 Acres	Sec. 25 Acres	Sec. 23 Acres	Sec. 19 Acres	Sec. 24 Acres	Total Acres	Total Percent
Pasture	125	60	45	60	70	10	145	15	140	670	26.13
Corn	60	35	15	50	10	95	20	70	175	530	20.67
Beans	30	15	..	15	35	105	..	10	60	270	10.35
Plowing	35	10	20	5	..	50	20	90	50	280	10.92
Clover	25	20	..	..	30	10	80	45	145	355	13.84
Farm yards	20	10	..	..	5	..	15	10	25	85	3.31
Town	20	..	..	20	..	..	..	40	15	95	3.70
Wheat	5	..	..	..	..	..	..	..	..	5	.19
Timothy	..	5	..	..	..	..	20	40	..	65	2.53
Oats	..	5	..	10	10	50	..	..	..	75	2.92
Wood Pasture	..	..	80	..	..	..	20	..	10	110	4.29
Alfalfa	..	..	..	..	..	..	..	..	15	15	.58
Sorgo	..	..	..	..	..	..	..	..	5	5	.19

farm buildings are not evenly distributed over the area. They range from seven sets on section 19 of the east-central side to only one group of buildings on section 27 of the west-central side. All of section 19 is under cultivation except for the farm yards while less than 25 acres of section 27 has ever been plowed.

Livestock farming is the general type of agriculture followed on the area. Sheep, beef cattle, hogs and to some extent horses and mules are raised. Corn, soy beans, hay and oats are the principal crops grown. Most of the crops are marketed through the livestock with the exception of soybeans which is a cash crop.

There are no natural barriers such as large streams or dense woods to restrict the free movements of skunks on or near the area but numerous tiles and tile-fed creeks on the east, northeast and west side of the area provide natural travelways for opossum *(Didelphis virginiana)*, mink *(Mustela vison)*, and are used to a lesser extent by muskrat *(Ondatra zibethicus)*, racoon *(Procyon lotor)* and other animals of the territory. The striped skunk *(Mephitis mephitis)* is always present in small numbers on the "rougher" portions of the area. Both red fox *(Vulpes regalis)* and grey fox *(Urocyon cinereoargenteus)* were killed on the area during the investigation period but they are not common.

Numerous hedges of osage orange *(Maclura pomifera)* are on the area, but are fast disappearing as they are being cut for posts and being grubbed out to make possible closer cultivation to fence lines (Fig. 5). These hedges provide excellent den sites and excellent cover for many types of wildlife. Woodchucks *(Marmota monax)*, especially numerous along the hedges, dig dens which are utilized by cottontails *(Sylvilagus floridanus mearnsii)*, skunks, opossums, and other mammals. Cottontails were present in varying population densities during the years of this study. They were most numerous during 1939 when the population was estimated as high as 4.5 per acre of feeding range (Hendrickson 1939). In 1941 the population was "about one-tenth as high as the peak in 1939" (Hendrickson 1941).

FIG. 5. A forty-year-old hedge on the west side of section 24.

Several coveys of quail *(Colinus v. virginianus)* were resident on the area but never in numbers comparable to those on "rougher" parts of the same county. A few pheasants *(Phasianus colchicus torquatus)* were resident on the northeast one-fourth of the area through the period of this study.

The great horned owl *(Bubo virginianus virginianus)* and the northern barred owl *(Strix varia varia)* are permanent residents in the wooded parts of the skunk area. Individuals of both species are frequently shot by farmers and hunters. The eastern screech owl *(Otus asio naevius)* is a common resident especially about farm yards.

The northern red-shouldered hawk *(Buteo lineatus lineatus)* and the eastern red-tailed hawk *(Buteo borealis borealis)* are fairly common summer residents on the area, and a few red-tails may stay throughout the winter. The eastern sparrow hawk *(Falco sparverius sparverius)* is a common summer resident.

Among the ground nesting birds the eastern meadow lark *(Sturnella magna magna)* and the prairie horned lark *(Otocoris alpestris praticola)* are the most common. The upland plover *(Bartramia longicaudata)* nests regularly on the area (Crabb 1939).

No attempt was made to take a census of small mammals on the skunk area but the following species were most numerous wherever suitable habitats existed for them: little short-tailed shrew *(Cryptotis parva)*, large short-tailed shrew *(Blarina b. brevicauda)*, thirteen-striped ground squirrel *(Citellus t. tridecemlineatus)*, prairie harvest mouse *(Reithrodontomys megalotis dychei)*, Baird white-footed mouse *(Peromyscus maniculatus bairdi)*, northern white-footed mouse *(Peromyscus leucopus novaboracensis)*, Pennsylvania meadow mouse *(Microtus p. pennsylvanicus)* and prairie meadow mouse *(Microtus ochragaster)*. House mouse *(Mus m. musculus)* and Norway rat *(Rattus norvegicus)* were generally common residents about farm buildings. Goss lemming mouse *(Synaptomys cooperi gossii)* was collected on the area but it is exceedingly rare.

During the years 1939, 1940 and 1941 the annual mean temperatures at Stockport were 52.6, 49.6, 53.3, respectively. The total annual precipitation for these years respectively was 34.65, 29.27, 39.11 inches (Reed 1939, 1940, 1941). These data originated at a federal weather station located almost in the exact center of the skunk area. The elevation at Stockport is 747 feet.

FIELD TECHNIQUES

A thorough knowledge of the habits of the spotted skunk and methods of handling it, or even associating with it, are prerequisite to a successful investigation of the species. Spotted skunks are highly nocturnal and secretive in their habits and endowed with keen senses of smell and hearing.

In agreement with others (Seton 1937) the writer has never seen spotted skunks abroad in daylight of their own free will, but they are sometimes ousted from their daytime hiding by dogs and men about farm yards where they frequently make their homes. They probably do come out on occasion in broad daylight in good health and of their own free will. Numerous reports of seeing them have been made on the research area but on careful investigation most of the reports were proven not reliable. One reported incident may serve as an exception.

A farmer in March butchered two hogs between a garage and washhouse in the yard. It was a cool bright day; the temperature was a little below freezing and there was about one and one-half inches of snow on the ground. The butchering was completed at noon and the hogs were left hanging to cool until evening. That afternoon a spotted skunk came out from under the washhouse a dilapidated old building with a wooden floor, and foraged among the blood and butchering scraps for food. Although only one little skunk was seen at a time the farm family watching from a kitchen window expressed the opinion that there were two or three different animals.

In this instance several factors ought to be considered. First, the skunk evidently had a den under the washhouse; second, it was probably hungry for food, more difficult to get at this time of year than any other time (Crabb 1941), and lastly, the butchering was probably done within eight or ten feet of the den nest and the odor of fresh meat and warm blood in such abundance was too much to resist.

Because of the practical impossibility of direct observation of the activities of the spotted skunk, indirect observation, that is by evidence of activity or live trapping, must be relied upon for information.

SIGN OF THE SPOTTED SKUNK

One of the best signs of the spotted skunk is its fecal passages (Fig. 6). They seldom make latrines and where they do appear they serve as indicators of nearby dens or may even be in the dens (Fig. 7). As a rule the skunks defecate promiscuously except in their nests. Where they use barns, scats may be found all along the runways, which usually follow rafters, poles and brace pieces. Where the animals are using board or firewood piles scats may be picked up anywhere nearby. They defecate freely about farm yards on bare patches of ground and often

leave their scats within a few feet of their day-time nest when leaving it for the nightly forage. Cow paths, dry washes in fields, fence lines and even low grave stones are likely places to find scats.

These scats when found suggest many things, such as: what the animal has been eating and hence where to look for feeding sign: how recently the animal has passed this way from the probable age of the scats; and how frequently or intensely the place is used by the number of scats to be found. Several characters must be considered when determining the identity of scats. Size, shape, contents, and odor are indicators of their origin (Crabb 1941).

FIG. 6. Characteristic summer scats of spotted and striped skunks.

FIG. 7. A spotted skunk latrine between the hay and the side of an old barn.

Evidence of feeding left on and about various food items is a source of much information not to be overlooked when working with the spotted skunk. Methods of attacking living prey, particularly parts and amounts consumed; methods of eating, such as in egg-eating; and location of the food items usually conform to particular patterns with this species as well as with other predaceous species, such as the red fox (Scott 1943).

During June of each year many great ragweeds *(Abrosia trifida)* were found nearly uprooted in vast numbers by skunks in search of scarabaeid beetles at the roots. Eggs eaten in and about farm buildings usually have one end or a side broken out. The shell is usually clean cut and the contents lapped up and cleaned out in a manner impossible for a bird but not much unlike a cat (Fig. 8).

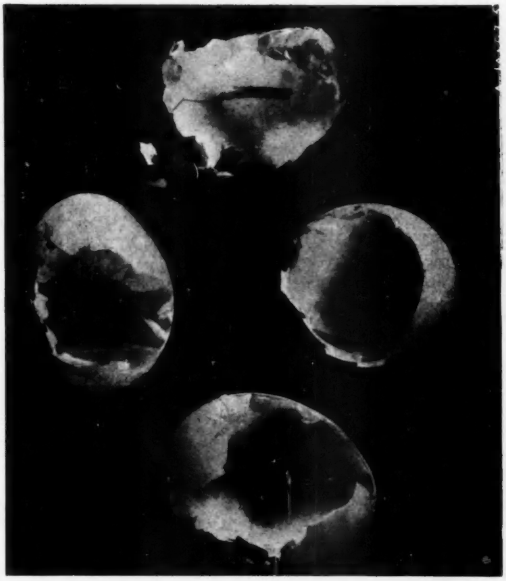

FIG. 8. Domestic hen eggs eaten by spotted skunks during May, 1942.

Rabbits, chickens, and pheasants eaten as carrion are ordinarily dragged to the den entrance or protective cover to be eaten (Figs. 9, 10). There scats may be found to confirm suspicions. The large bones of these species are not eaten, feathers are pulled out and scattered about, not sheared off, and usually more than one visit will be made to a carcass on successive nights. The unlikeliness of other mammalian carrion eaters feeding under such circumstances on an area well known to the invest'gator is profitably used in deductive reasoning.

During the winter months tracking is one of the most positive signs of the skunk's presence and activity. During the other seasons a few tracks may be found in the mud after a rain or along wet creeks.

The tracks are of several types depending upon the speed the animal is making and the method of

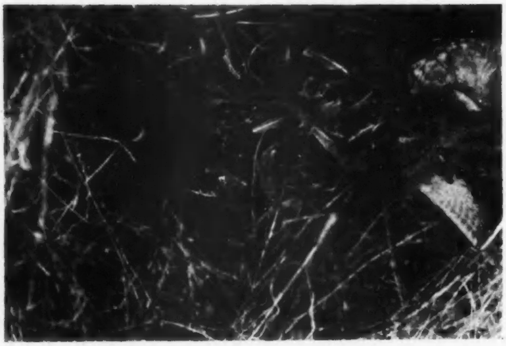

FIG. 9. A pheasant carcass at the entrance of a spotted skunk den in an alfalfa field.

FIG. 10. A rabbit carcass dragged under the end of a culvert and partially eaten.

FIG. 11. Tracks of the bounding spotted skunk in the snow.

FIG. 12. Tracks made by a galloping spotted skunk crossed with tracks of an opossum.

travel. While hunting the animal may be walking. The hind feet are then placed exactly in the print of the front feet and the steps are made at five or five and one-half inch intervals depending upon particular individuals. By far the most common gait in the field while hunting is a bounding gait. Here the front and hind feet work in pairs after the manner of weasel and mink (Fig. 11). The distance between tracks may vary from nine to fourteen inches depending upon the rate of progress and size of the animal. Another track frequently made results from a galloping gait. In this the tracks are more like those of the striped skunk in that the front feet tracks do not register perfectly with those of the hind feet (Fig. 12). This gait, as the others may be used at varying rates of speed and with different distances between tracks ranging from seven to ten inches.

The feet of the spotted skunk are similar to those of the striped skunk. A part of the sole of both the front and hind feet is applied directly to the ground. The claws on the fore-feet are moderately long and those behind quite short (Fig. 13). The front feet are well adapted to grasping and the spotted skunk is quite adept at climbing trees after the manner of weasels and minks (Fig. 14).

Another reliable field sign for the spotted skunk as well as other animals is the hairs left about den entrances or other holes such as those forced into chicken coops for the purpose of predation on rats or chickens. By using a magnifying glass and check specimens, hairs often serve as excellent conclusive evidence.

A useful hair-catching device was placed at the entrance of many holes where more detailed information concerning the inhabitants of the hole was wanted (Fig. 15). It was made from a piece of tin can about three inches by two inches by serrating an edge. The serrations were made by cutting one-half inch into the tin with a pair of tin snippers at about every one-sixteenth inch. If carefully made and nailed in place it does not obstruct the opening and will catch hairs of the animals entering and leaving. The device yields information on the frequency of use of a particular den, as well as providing clues for the accurate identification of the species.

An excellent field sign when it is present is the odor of the musk. With a little experience and a reasonably good "nose" one may differentiate be-

tween the musks of striped and spotted skunks with almost 100% accuracy. About farm yards this little skunk is interfered with or attacked by dogs and cats and where this is encouraged by the farmers there may be a constant musk odor about the premises. The spotted skunks frequently emit a small amount of musk when engaged in vigorous fights with rats or in rough and tumble play among themselves. Lants (1905) also mentioned the slight odor left by the little skunks. ". . . on the mornings after an unusually fierce battle with rats, I could detect a faint smell of its presence in the cellar."

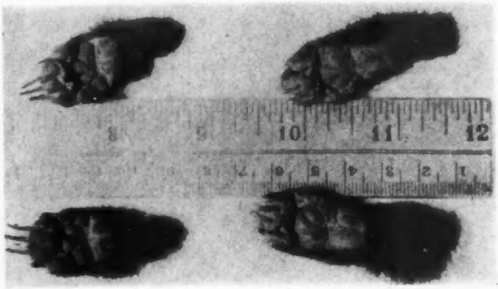

FIG. 13. Feet of a large male spotted skunk.

FIG. 14. Spotted skunk high in a tree where it went after being released from a trap.

As with other animals, characteristic odors are to be associated with the spotted skunk other than the musk. One is frequently aware of the presence of this skunk about a premise long before more concrete evidence is found. A musty odor of concealed scats and of a long used nest frequently permeate old buildings, barns and woodpiles. A nest of young spotted skunks and the associated runways in a house may have so strong an odor as to make living in the part of the house affected uncomfortable. The characteristic den odor has no resemblance to the anal musk and consequently it is frequently not associated with the spotted skunk by the uninformed.

However, the den odor is not usually offensive. A country schoolhouse (Fig. 16) at Stockport, in which spotted skunks have been established for many years both in the attic and basement, never became offensive although scats were all over the attic floor to a depth of an inch in many places.

TRAPPING AND TAGGING

The successful trapping and ear-tagging of spotted skunks rests upon a specialized technique and a thorough understanding of the habits and disposition of the animals (Crabb 1941a).

The traps used in this study were designed especially for the capture and handling of spotted skunks with a minimum of risk to the operator and as much protection as possible for the animal (Fig. 17). Protection of the animal against the adversities of weather and attacks by domestic animals is of pri-

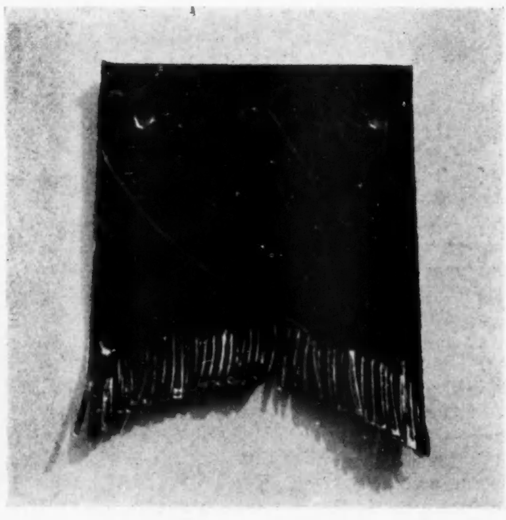

FIG. 15. Serrated piece of tin fastened over holes to catch hair of inhabitants.

FIG. 16. The "Frog-pond" Schoolhouse at Stockport. The attic and wall have been used by spotted skunks for many years.

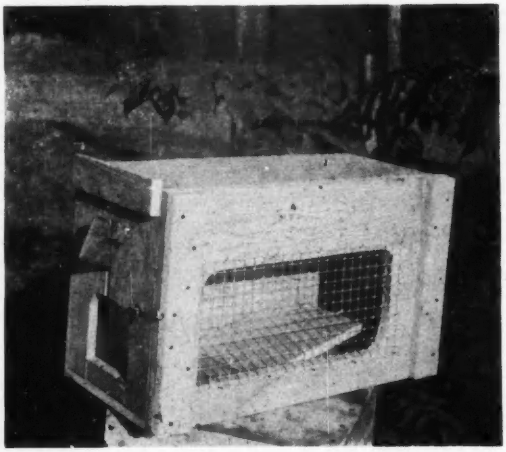

FIG. 17. Box trap used to catch and handle spotted skunks.

mary importance if the little skunks are to be released unharmed. The desirability for protection on the part of the operator is obvious.

Spotted skunks, like striped skunks, are usually considered easy to catch by fur-trappers and individuals attempting to control them. In general this is correct as it applies to the skunks during the fur-trapping season, but during other times of the year, especially during late spring and early summer, they are difficult to catch.

During the winter months the food eaten is largely rats and mice. At this time a meat bait was taken readily and with it trapping was comparatively easy. During the late summer and fall fruit made a good bait, especially when used in conjunction with regular feeding places of the skunks; for example, mulberries under a mulberry tree.

During late spring and summer trapping was difficult. The diet at this time is almost entirely insects, for insects of many kinds are abundant and widely distributed. Feeding of them does not confine the skunk to any one area and very little hunting about is required to get a full meal. Consequently the skunks are seldom hungry and like other animals when well fed are tempted by nothing but the choicest morsel.

Using the quadrat system of trapping for 1,160 trap nights during February, 56 spotted skunks were caught. Trap sets were 4.8% successful. The bait used during this period was small pieces of rabbit meat with a drop of lure (fish oil and musk) in each trap. These traps also caught 13 cats, three cottontails, four opossums, two striped skunks and one Norway rat for a total success of 6.8%.

During a three-weeks period in late April and early May covering 778 trap nights 21 spotted skunks were caught. These sets were 2.7% successful. These same traps caught two cats, five rabbits, one rat and two brown thrashers *(Toxostoma rufum)*. These traps also contained a drop of the lure (fish oil and musk) but the baits were varied. Canned mackerel, honey, egg, and rabbit meat were used as bait in conjunction with the lure. The traps were frequently covered with mud to conceal odors and blend them with the surroundings.

When trapping was first used on the Stockport area the emphasis was placed upon getting as many of the skunks caught and marked as possible regardless of the methods used or the irregular coverage of the area. A system of "spot" trapping was employed. From 10 to 20 box traps were available and these were concentrated on two or three spotted skunk locations such as in two or three farm yards. The traps were moved to new locations once or twice a week. This method provided sufficient time to search carefully for skunk sign and tended to hold the success per trap night at a comparatively high level. Later it seemed that a more careful and complete coverage of a smaller area, and a smaller part of the total skunk population would be more fruitful.

To this end the number of traps was increased to 68 and a full-time technician was employed to help in tending them. Sixty-four of the traps were then placed on 640 acres of the area, one trap to each 10 acres. The traps were visited every other day unless weather made a more frequent check obligatory. The traps were usually reset and rebaited when visited and they were moved about in their respective 10-acre quadrat once each week.

After about one month of such trapping it became obvious that not enough area was being covered and what was being covered was being trapped too intensely. This was evident from the large number of spotted skunks represented by single catches and the small number caught many times. In other words the trap area did not cover enough unit ranges. Trapping was also so intense that two or three spotted skunks died from frequent exposure in the traps and others were noticeably weakened. The trap plan was then enlarged to cover four central sections of the area. The four sections consisted of the original central section, the bordering one-half sections along the sides and the one-quarter sections at the

corners (Fig. 1). Thirty-two traps were left on 320 acres of the central section at all times and the other 32 traps were used on 320 acres of the bordering land. These traps were moved at three-week intervals from one quadrat to another in such a manner that the central sections received twice as much trapping as the bordering sections and all four sections were completely covered each season of three months (Fig. 18).

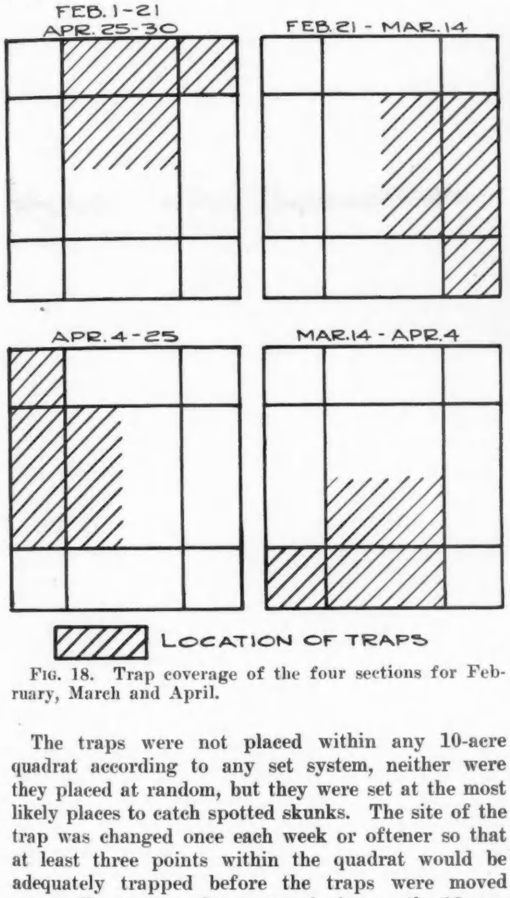

FIG. 18. Trap coverage of the four sections for February, March and April.

The traps were not placed within any 10-acre quadrat according to any set system, neither were they placed at random, but they were set at the most likely places to catch spotted skunks. The site of the trap was changed once each week or oftener so that at least three points within the quadrat would be adequately trapped before the traps were moved away. Traps were placed at such sites on the 10-acre tracts as past experience indicated might be used by spotted skunks. In this manner trapping adequately covered all the probable skunk habitat.

This method of setting compensated somewhat for the difficulties encountered when the 10-acre quadrat was bare land such as plowed grounds or heavily pastured fields which if trapped according to a measured system would only rarely catch a skunk coming on to the quadrat unless a larger number of traps could be used.

After a skunk was caught it was placed in the tagging chute and one "Salasco" fingerling tag (made by the Salt Lake Stamp Company, Salt Lake, Utah) was placed in each ear. It was essential to see that the tags were well clinched and did not pinch the ear for when they did they caused infection and were lost. The animals were weighed, searched for external parasites, their sex noted and any other pertinent data, such as evidence of sucking females, absence of toes on feet or evidence of age, recorded (Fig. 19). The date, location, and bait used were also noted.

FIG. 19. The author ear-tagging a spotted skunk in the tagging chute.

SPOTTED SKUNK HABITAT

One of the major objectives of this investigation was to uncover some of the facts concerning territories and the constituents of the habitat of the spotted skunk.

THE DEN OF THE SPOTTED SKUNK—A REQUIREMENT

While gathering data for this investigation a den was considered to be "any location or cover which the animal uses of its own free will for rest or seclusion."

This little skunk was as adaptable in its choice of a den as it was in its choice of food (Crabb 1941). The first consideration seems to be the exclusion of light. Without exception every den or semblence of a den met this requirement. Sometimes the den was only a place to curl up or stretch out in such as under the corner of a well platform or a shock of small grain, but wherever darkness prevailed there the spotted skunk seemed to feel most at home.

A second important requirement is protection against weather conditions. They must have protection against summer heat, winter cold, wet rains and snow, and cold winds. The variety of places meeting these conditions was almost unlimited about the farms and fields of southeast Iowa.

A third requirement, although not always carefully considered, is protection against "enemies"—dogs, men and livestock. About 50% of the total mortality reported in this paper was directly traceable to a careless choice of a den in this respect.

The provision of more den sites meeting these three requirements suggests itself as a possible management practice for the species. Farm buildings of all types

from the house to the outhouse were used freely for dens. Most of the buildings at Stockport are built loosely and few are completely inclosed. Almost all rest upon loose limestone rocks and few houses have basements for the ground water level is commonly within three feet of the surface during spring and fall. Any building accessible to a rat is equally accessible to this little skunk for it is remarkably adept at following rat runways.

Seton (1937) says the following concerning the dens of the spotted skunk:

> The den is often a natural cavity in the rocks, or a convenient crevice under a stone pile, but sometimes a hollow log or a stump is used. Out on the plains or other level lands, the Spotted Skunk often digs a burrow for itself under the cactus and thorny underbrush; or more often, it uses the deserted burrow of some other animal, such as a Ground-squirrel or a Woodrat, or in Florida, even that of a burrowing owl. . . . I found one living merrily among the vast food possibilities of a grain elevator. So far, no one has reported the nest in a wet place or high up in a hollow tree.

On July 5, 1939 while investigating a large soft maple tree *(Acer saccharinum)* that had blown down the night before in a storm, a hollow was located containing scats and hair of the spotted skunk. The entrance to the hole was at least 20 feet from the ground.

FIG. 20. Entrance to a summer den in a hollow-tile walk at an abandoned farmstead.

FIG. 21. A rotting strawpile at Stockport in December, an excellent den for spotted skunks.

Pellett (1913) found a nest under a pile of cobs in an outbuilding. Strawpiles, hay stacks, hollow trees and hollow logs—especially in hedge rows, firewood and board piles of all kinds, junk piles, hollow tiles, drainage tiles, old well and appropriated ground dens of other species were all used for dens (Figs. 20, 21, 22, 23).

FIG. 22. Den in a hollow tree used during the summer of 1939. The boy points towards the entrance.

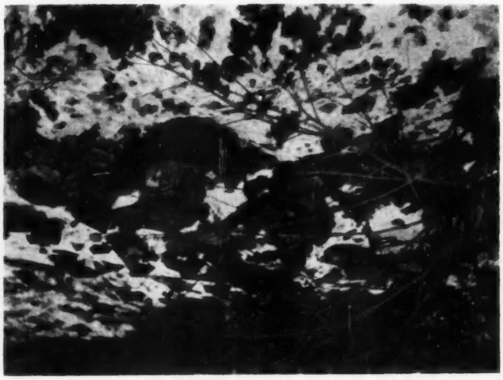

FIG. 23. Den of woodchuck at an old building site used by spotted skunks in December, 1938.

Very few ground dens were used and fewer were made by the spotted skunk. One ground den was the enlarged burrow of the 13-striped ground squirrel and was used during winter months (Figs. 24, 26). Another was appropriated from a long tailed weasel *(Mustela frenata)* and others from striped skunks and woodchucks (Fig. 25).

As this investigation was primarily concerned with studying the mobility, territory and general environment of the spotted skunks every effort was made to avoid altering the natural situation or forces influencing their behavior; consequently few dens were opened or disturbed.

A survey of permanent and semi-permanent den sites was made of 78 farm yards of the area in the spring of 1942. The farm yards were classified for

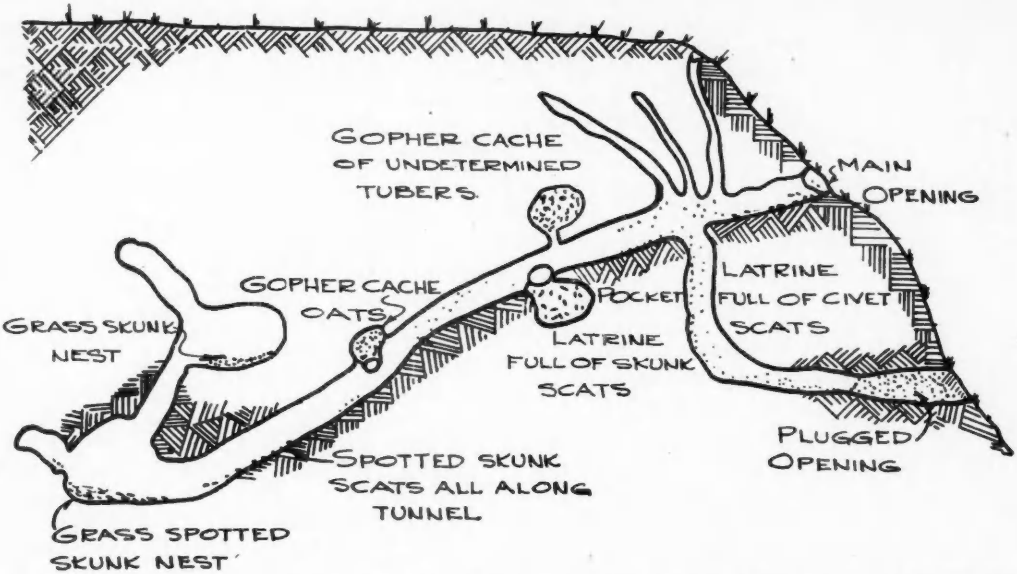

FIG. 24. Ground den of spotted skunk enlarged and taken over from 13-striped ground squirrel. Opened February 26, 1940. Scale ¾ in. = 1 ft.

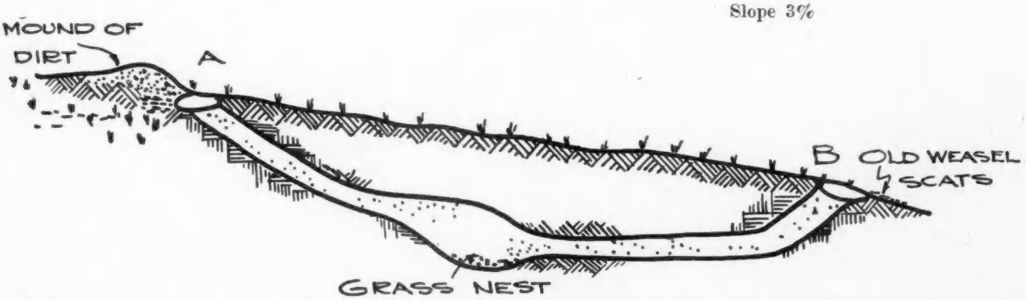

FIG. 25. Ground den used by female spotted skunk and five young. Opened July 21, 1941. Evidently it originally belonged to a weasel. Scale ¾ in. = 1 ft.

FIG. 26. Entrance to ground den January 30, 1940, illustrated in Fig. 31. Note the tracks in the snow.

convenience into the following three catagories: Fair—one den site, good—two den sites, and excellent—three or more den sites. Forty-eight (60%) of the farm yards came into the "excellent" classification with three or more permanent or semipermanent den sites. Twenty-three (29.44%) came under the "good" classification. Six (7.68%) were classified with only one possible den site and only one farm had none. This was a very conservative estimate based upon four years of observation and a personal check at the time of rating and it does not take into account those necessarily over-looked because they could not be found.

These farm yards are located on 14.75 sections of the 17-section area. This then provided an average of 5.3 farm yards per section with a minimum of 196 den sites on the 14.75 sections for an average of 13 permanent and semi-permanent dens per section. These dens were exclusive of 20 or 30 provided by

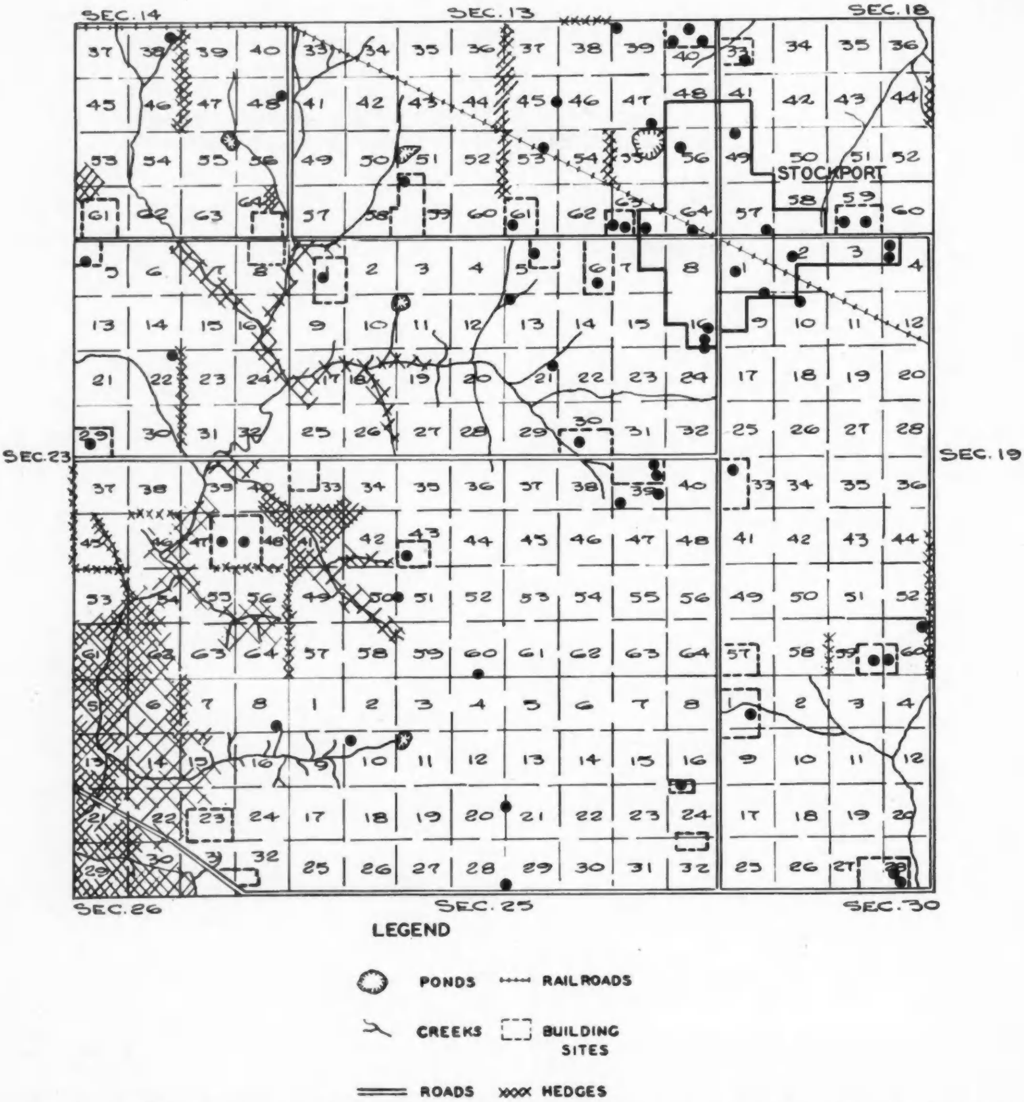

FIG. 27. Distribution of active dens of the first five months of 1942, on four sections of the Stockport area. Each black spot represents a den location.

the town in the northeast corner of the area. It must be understood, too, that the calculation of permanent and semi-permanent den sites did not include strawpiles, hay piles, tiles, hollow trees, hedges, junk piles and other field dens not directly related to the farm yard proper.

This large number of den sites would probably never be available to spotted skunks on the native prairie. Cultural practices have had little tendency to deplete prairie den sites and at Stockport drainage has made many more possible. Besides field dens agriculture had provided a vast number of new den sites about buildings and accumulations characteristic of Iowa farm yards.

During the first five months of 1942 four sections were under intensive observation and quadrat trapping. Sixty different dens were used from one to five months during this period of the four-section area. Of this total only eight were not directly related to some phase of agricultural activity (Figs. 27, 28, Table 9).

Crop storage buildings such as granaries, barns and corncribs provided 31 dens (51.46%) of the dens used during this period and 106 den-months with an aver-

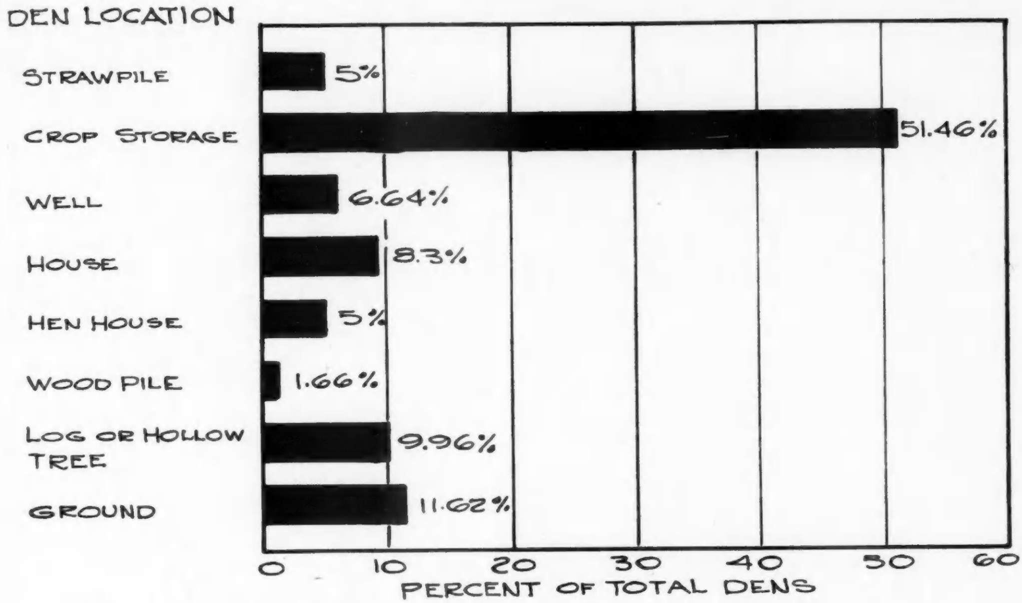

FIG. 28. Sixty dens used from January to May, 1942, on four sections.

age active-use period of 3.4 months. Hollow trees and hollow logs provided six dens (10%) of those used during the period and had an average of 3.1 months use; and houses provided five dens (8.3%). The average use was 3.6 months. Open shallow wells with limestone rock curbings and ground dens provided 11 dens (18%) of the total. But the period of active use was less than the other categories with an average for both types of 2.5 months. These dens were largely used during late spring. Strawpiles and chicken houses provided three dens each (5%) with an average use of 3.6 months.

Dens and den sites distributed over the area seem to belong not to any one skunk or family of skunks, if such exists, but to the whole population. Exceptions should be made for those used by the mother for a brood chamber during the breeding season. The spotted skunks move about from farm yard to farm yard and from den to den as suits their inclinations. That several may be using the same den is well known to trappers. During the fall trapping season it is not uncommon for a trapper to catch from three to six or seven spotted skunks at one den. The existence of family ties may be a contributing factor although by this time family dispersal is probably completed. However, the use of a den during the spring by a number of skunks can hardly be attributed to such a cause. On April 23, 1939 four males and one non-breeding female were trapped or killed by poison under a farm house at Stockport. At various times during the spring and summer from two to three spotted skunks have been seen in the attic of the "Frog-pond" schoolhouse (Fig. 16). While trapping in quadrats during five months of 1942 two or more skunks were regularly caught at the same den. At one hollow post den in a field three males and one female were caught in a period of five nights during April.

DEN CHARACTERISTICS

All of the ground dens opened contained a nest of grass or hay and those in buildings were frequently built in hay or between hay bales (Fig. 29). The attic of the schoolhouse, however, had no nest material. The spotted skunks curled up in corners between the eaves and the plate or corners of the rafters supporting the ceiling. The nests in wood piles and under well platforms seldom had nest material but these were generally warm weather dens when such material was less essential.

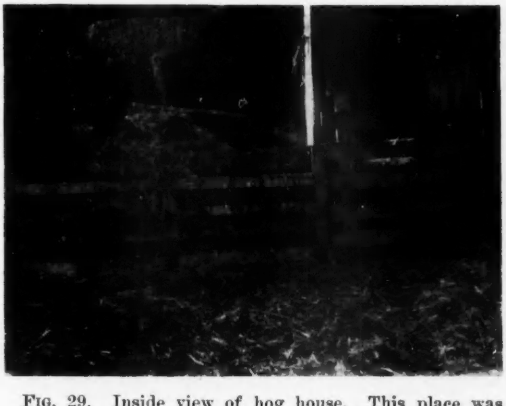

FIG. 29. Inside view of hog house. This place was used as a den all winter and spring of 1942.

Scats are commonly scattered along all the runways leading to and from the dens (Figs. 24, 25). The scat accumulations in some dens often reach remarkable proportions. In attics and walls where dens had been long established they were from one to three inches deep.

The "Road" Between

One of the fundamental features of a good den site is its safe accessibility. A building more than five or ten rods from a fence and surrounded by bare or closely grazed ground was seldom used by the spotted skunks. On the other hand those buildings adjoining fences, wood piles, other buildings, or farm yard accumulations, were almost invariably inhabited, even in the face of stiff opposition on the part of a farm dog and farmer prejudice.

One farm yard on the area had many dilapidated buildings, eight or ten wood piles, several antiquated strawpiles, five or six junk cars, and was shaded by many old hollow maple, walnut *(Juglans nigra)*, and mulberry *(Morus rubra)* trees. It was managed by a widow and maintained a resident spotted skunk population throughout the course of this study, although an aggressive collie dog and the woman pursued them at every opportunity and killed several every year. Contrasted with this was a carefully kept farm yard in which the machinery was always kept in sheds, weeds cut, and grass mowed about the place with a lawn mower. This place never had a spotted skunk den in the course of the investigation.

Direct observation of skunk activity and indirect observation by following tracks gives the best evidence of "road" use by the spotted skunks. In the summer of 1939 skunks were using a wood pile that could be easily approached by an automobile. Several nights were spent in watching two adult spotted skunks come out of this wood pile for their nightly forage (Fig. 30). The quite noisily stumbled over the loose blocks of firewood, paused at the edge of the pile, then cautiously crept through the short grass to the "safety" of a hay wagon where they stopped momentarily, sniffed the air and listened, before sneaking over to an old corn cultivator and repeating the listening and sniffing before proceeding. This went on until they were lost to view. At a slight movement in the car they would "freeze" in their tracks, elevate their tails prepared for defense and would hold that pose until satisfied of their safety. When they stopped if they were not definitely "marked down" it was virtually impossible to distinguish their forms in the dusk or moonlight.

Tracks in the snow in the vicinity of dens invariably led along fence lines, through brush piles, under farm machinery, skirted foundations of buildings and followed drainage lines. These "roads" of "in-between" or escape cover serve other purposes besides safety for it is along fence rows, in the brush piles, and in the weed patches that food is to be found. Mice, insects and fruit are all abundant at various times in such places. The use of such "roads" may be often more accurately attributed to food hunting than a desire for safety. However, it ought to be said that such roads are essential about dens where pursuit by enemies is a daily consideration.

FIG. 30. A large woodpile used by spotted skunks for a summer den, 1939.

Lethal Pressure and Den Usage

Certain dens served admirably under all conditions as long as they were not discovered by unfriendly men or dogs. A den may seem to have been ideally located in the midst of abundant food and protective cover, it might be warm and dry and perfectly safe from intrusion, but if it was frequently worked by a dog scratching, clawing, digging, and barking about its entrance it was quickly vacated. Likewise human activity about the opening such as plugging or smoking the den soon discouraged its occupant, who moved to other quarters. Such dens bear watching by the investigator for in two to three weeks they may again be occupied. The occupant might be another individual, but the odor of previous occupancy seemed to mark a den indefinitely for future passers-by. Probably one of the mose useful management practices is the discouragement of dogs when they "tree" a skunk about farm yards.

Physical Requirements of the Species

A den site to be habitable must provide in the den and in its vicinity the physical needs of the animal during some particular time. Many places serve as dens during the summer when severe changes in weather are not expected and sleeping "outdoors" is a practice indulged in by most animal life. A shock of oats, a few boards piled up, a large tuft of grass, which a cottontail might use for a form, or a cool spot under a baby chick coop served admirably as summer sleeping quarters. During winter or early spring when ground dens were flooded, snow and ice and cold winds were regular, exposure in this type of den would kill the animal. Then the warm interior of a barn, straw stack or a house were much preferred.

Of equal importance is the availability of foods. Spotted skunks seem to have two general types of range behavior, that is, winter and summer. Winter range seems to be determined by needs for food and

shelter, and summer range is probably indeterminate by reason of great abundance of food and wide dispersion of cover and den sites. During winter, mice, rats, rabbits, and corn were the principal items of diet. These foods were to be found in abundance about farm yards on the area. These foods in conjunction with suitable sleeping quarters are of considerable importance to an animal that must eat regularly during all kinds of weather. The proximity of food probably was a deciding factor in the choice or rejection of building dens for winter habitation.

When warm weather returns, food probably ceases to be a deciding factor in the use of dens for this skunk is an omnivorous animal with a decided preference for insect food. The prevalence of such food supplemented at times with a long list of other foods all over the area made possible the use of any prospective den site and likewise had no tendency to limit the activity of the skunk to any one vicinity or any one den.

As data accumulated and was reviewed it became increasingly apparent that the word "territory" with its implications of defence and advertisement, in the sense used by Nice (1941) and others with regard to birds and other vertebrates, can hardly be applied to the habitat pattern of the spotted skunk for the elements of defense or advertisement never seemed to be factors. An expression "area of familiarity" seems more descriptive of the spotted skunk's domain. Any particular part of the area of familarity serves the little skunk only so long as it suits him. When it no longer provides the necessities of life to his satisfaction he moves on. He may move into another part of his previous area or he may extend his familiarity to new and unexplored ground. The fact that other skunks move in on him or that he moves in on others probably makes no great difference to him.

A place to sleep, reasonably secure from dogs, men, and daylight; availability of any of a large number of foods, animal or plant; and chances of a reasonably safe passageway between the two seem to be the basic factors regulating the limit of usefulness of any part of the area of familiarity.

POPULATION

Population Density

During the course of this investigation of 39 months, 238 individual spotted skunks were known to have used the stockport area. Assuming a complete change of population each year the known skunks on the area would allow for 79 individuals per year or slightly more than 5.6 per square mile for the 14 square miles of the 17-section area on which individual spotted skunks were handled. It is definitely known, however, that a complete change of population does not take place and that a certain portion of the population at any one time is made up of juveniles or short yearlings and another portion of adults and aged animals. It must also be remembered that the number of skunks killed about the farms was never completely recorded and no account whatever was made of those dying natural deaths from disease or old age.

The figures most indicative of population density are those that represent the skunks caught on the central four sections the first five months of 1942.

TABLE 2. Den locations on four sections Jan., Feb., Mar., Apr., May, 1942.

Den Location		Total Number Of Dens	Total Months In Use	Percent Of Total Dens	Average Number Months Used
Strawpile	Number 1 1 1 Months Used 5 4 2	3	11	5	3.6
Crop Storage	Number 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 Months Used 2 3 3 3 4 3 5 3 5 5 5 2 3 5 5 2	31	106	51.46	3.4
Crop Storage	Number 1 1 1 1 1 1 1 1 1 1 1 1 1 1 1 Months Used 5 4 3 3 3 3 3 3 1 2 3 5 2 5 3				
Rock Wall Well	Number 1 1 1 1 Months Used 5 3 1 1	4	10	6.64	2.5
House	Number 1 1 1 1 1 Months Used 5 3 5 2 3	5	18	8.30	3.6
Chicken House	Number 1 1 1 Months Used 4 5 2	3	11	5	3.6
Woodpile	Number 1 Months Used 5	1	5	1.66	5
Log or Hollow Tree	Number 1 1 1 1 1 1 Months Used 3 2 5 3 2 4	6	19	9.96	3.1
Ground	Number 1 1 1 1 1 1 1 Months Used 5 2 1 1 5 3 1	7	18	11.62	2.5

It would be misleading, if not erroneous, to consider more than three months of the five month period because during January only one section was trapped and during May trap success fell off so sharply that many skunks on the area at the time were unquestionably not being caught.

During February, March, and April of 1942, 57 different spotted skunks were known to have used these four sections. Of a total of 30 caught during February, 12 were recaught during March and of 25 caught on the area during March, five were recaught during April. Also of the 30 caught during February six were recaught in April (Table 3). However, never more than two and one-fourth sections were ever trapped in any 30-day period so the numbers caught in any one month do not represent the population that used the four sections but only slightly more than one-half of it (Fig. 18). This accounts for the fact that almost equal numbers were caught during each month but that a number of different individuals were caught as the particular one-fourth of the area being trapped was changed. To state the situation more completely, it appears from the data that regardless of which part (two sections) of the area was trapped in any one month approximately 26 spotted skunks were caught. Dividing 26 by two results in 13 skunks per square mile which is believed to be nearly correct for the Stockport area in the late winter and early spring of 1942. This, of course, is not intended to imply that 13 spotted skunks were limited to each section but only that 13 spotted skunks used every square mile of those under observation.

TABLE 3. Population density. Spotted skunks caught on four sections during Feb., Mar., and April of 1940.

Skunk No.	No. of Times Caught			Skunk No.	No. of Times Caught		
	Feb.	Mar.	April		Feb.	Mar.	April
1	1	3	..	29	1	3	1
2	2	..	..	30	2	1	..
3	2	3	..	31	..	1	..
4	1	2	..	32	..	3	..
5	2	1	..	33	..	1	..
6	1	..	4	34	..	1	..
7	3	2	..	35	..	1	..
8	1	..	..	36	..	1	..
9	1	1	..	37	..	1	..
10	4	..	..	38	..	1	1
11	6	..	..	39	..	2	..
12	4	..	..	40	..	2	..
13	3	..	..	41	..	1	..
14	2	..	..	42	..	1	..
15	1	..	..	43	..	1	1
16	1	1	1	44	..	..	1
17	1	..	..	45	..	..	2
18	1	..	..	46	..	..	2
19	1	..	..	47	..	..	1
20	1	..	..	48	..	..	1
21	1	..	..	49	..	..	2
22	2	..	..	50	..	..	1
23	1	..	..	51	..	..	1
24	1	2	1	52	..	..	1
25	1	5	..	53	..	..	1
26	1	..	1	54	..	..	1
27	4	1	..	55	..	..	1
28	1	..	..				

It is undoubtedly true as Burt (1940) emphasized:

> In order to determine the population of unit areas for a given species, it is essential first to select an area larger than the normal range of an individual of that species.

Errington (1939) pointed out for similar investigations the value of areas "several times as large." As will be explained later this four-square-mile area probably is not much larger than the unit range of the individuals except during certain seasons (notably winter) and for certain sex groups.

The overlap of area being trapped undoubtedly accounts for some recatches each month. The overlap of ranges of individual skunks from one section to another accounts for some others. It must also be noted (Fig. 18) that the four sections were completely trapped over only once during the three-month period.

SEX RATIO

During the course of this investigation the sex of 176 spotted skunks was definitely determined. During 1940 sex records of 67 individuals caught in the traps were obtained with a sex ratio of 3.66:1 (52 males, 15 females). That year trapping was almost entirely dependent upon a commercial lure and it was probably selective. During 1941 and 1942, 76 skunks were caught in the traps with a wide variety of baits and lures. They had a sex ratio of 1.81:1 (49 males, 27 females).

Sex was determined on 26 spotted skunks killed by farmers and others on the area during the four years of the investigation. Their ratio was 1.6:1 (16 males, 10 females). The sex of three complete litters of young were obtained with a ratio of 1.3:1 (9 males, 7 females).

Disregarding the skunks caught during 1940 when almost four males were caught to one female, and the trapping was likely selective, the sex ratio of those killed, of those trapped in 1941-'42 and of the three litters was 1.68:1 (74 males, 44 females). This believed to be nearly correct for the spotted skunks on the Stockport area.

A sex ratio of 1.32:1 (49 males, 37 females) was reported on 86 spotted skunks killed by trappers in Missouri by Bennitt & Nagel (1937).

RANGES

The determination of individual ranges of spotted skunks is attended with many difficulties. As previously stated the animal is nocturnal to such a degree that direct observation is a practical impossibility. Indirect observation by means of tracks and feeding sign is good only during three or four days each winter. Dens of a particular type—excellent indicators of activity of some mammals—are unknown for this species. Feeding habits span such a wide range of vegetables and animals that no consistent pattern can be followed. Finally the range or area used by spotted skunks seems to vary greatly

TABLE 4. Spotted skunk records used in sex ratio determination.

		Males	Females	Total
Trapped	1940	52	15	67*
Trapped	1941–1942	49	27	76
Mortality	1939–1942	16	10	26
Litters	1940 (1)	4	0	4
Litters	1941 (1)	1	4	5
Litters	1942 (1)	4	3	7

* These were trapped by a selective method and are considered unsuitable for sex ratio computation.

with the season and the individual and this lack of consistency in individuals provides no clues for identification of particular ranges.

With these difficulties in mind the decision was made to attempt trapping and ear-tagging as a means of following individual activities. This too had its attending difficulties but they were largely overcome by the use of special equipment and by the hiring of extra help to run the traps. However the war came and other complications arose. It became increasingly difficult to work about Iowa farms where everything was so rigidly regimented to the war effort. Labor became scarce and hard to hold. As a result the systematic trapping program was only well started when it was discontinued.

During the course of this investigation 161 spotted skunks were caught, tagged and released on the Stockport area. One hundred nine of them were caught and tagged on four sections of the area and it is from this group that range and territory data are largely gleaned. Of the 109, 14 were animals that had lost tags. However, since they were usually recaught in seasons other than the one in which they were first tagged and as their sex was always known their behavior for any particular season serves as well as the others.

Since only six or seven individuals were followed for longer than a three-month period the consideration of seasonal activity relating to ranges is handled in groups. The males and females had noticeably different activity patterns, at least during the spring season, and hence each sex is charted separately and considered separately in the discussion.

Sixty-four individuals were caught only once on the area; four of these, however, were caught from one to three times off the area. Single catches may be due to itinerants but some at least are due to cessation of trapping activities and some others probably learn to avoid the traps (Fig. 31). Only 45 skunks were caught more than once on the four sections and hence provide a basis for outlining the individual ranges. Records of individuals caught off the central four sections are used in the discussion to supplement the data that appears on the charts whenever they are pertinent.

On the maps with imposed trap records straight lines serve only to connect points of capture and are not intended to indicate routes of travel or territorial limits. Crooked lines between points designate routes of travel.

The ability to move about within an area is dependent somewhat upon the physical abilities of the individuals involved. The rate of speed and the endurance of the individual are important influencing factors upon the distances traveled during any one 24-hour period.

The prairie spotted skunk moves quickly but its rate of speed is easily exaggerated. The trapping and releasing of animals has provided excellent opportunity for observing their rate of travel. When thoroughly motivated to do their best they can be followed at a brisk walk about four and one-half miles an hour. The commonly held notion that spotted skunks move faster than striped skunks is erroneous. Several of the striped skunks released on the area bounded off so rapidly that following them one had to break from a walk to a trot which may have been as fast as seven or eight miles an hour. (See description of tracks for gaits employed.) The length of time such a rate of speed can be maintained is probably not more than one-half hour. None were ever followed that long, for they invariably took refuge in a tree, brush pile, building or some other safe place after going a few hundred yards. This of course is mobility under pressure. When traveling "normally" such as on a feeding trip at night they may move very little if food is abundant and easy to procure. If food is relatively hard to obtain they may be on the move all night. Table 5 presents the data on mobility in one night as observed during the investigation. This table does not present any of the day to day mobility as revealed by trapping, as trapping interrupts the activity of the animal. Figure 32 is an illustration of the route traveled by a spotted skunk one January night.

Males in Winter

Winter is a time of comparatively restricted activity for spotted skunks. They have their dens in hay barns or similar buildings and find their food in the vicinity. As was brought out in the section on habitats they usually have two or more semi-permanent or permanent stopping places or nests in the vicinity of their central den and between these places they eat and sleep.

Eight males were followed closely during January and February of 1942 on the central four sections. Six of these were known to be regularly using barns for basic dens and in the vicinity of these barns they were regularly caught. During good weather they often made foraging excursions along fence lines and into the surrounding fields.

Snow tracking was never good during the winter of 1942 but an illustration of an excursion one winter night by a spotted skunk is presented in diagrammatic form from the winter of 1940 (Fig. 32) and is described in the following account. The second week in January, 1940, a male skunk came out of a barn, went 40 rods across a pasture and into a cornstalk field. There it hunted over about four acres and then went south into an uncut timothy-hay field and thoroughly hunted over an area of about five acres. In the timothy-hay field it caught one meadow mouse

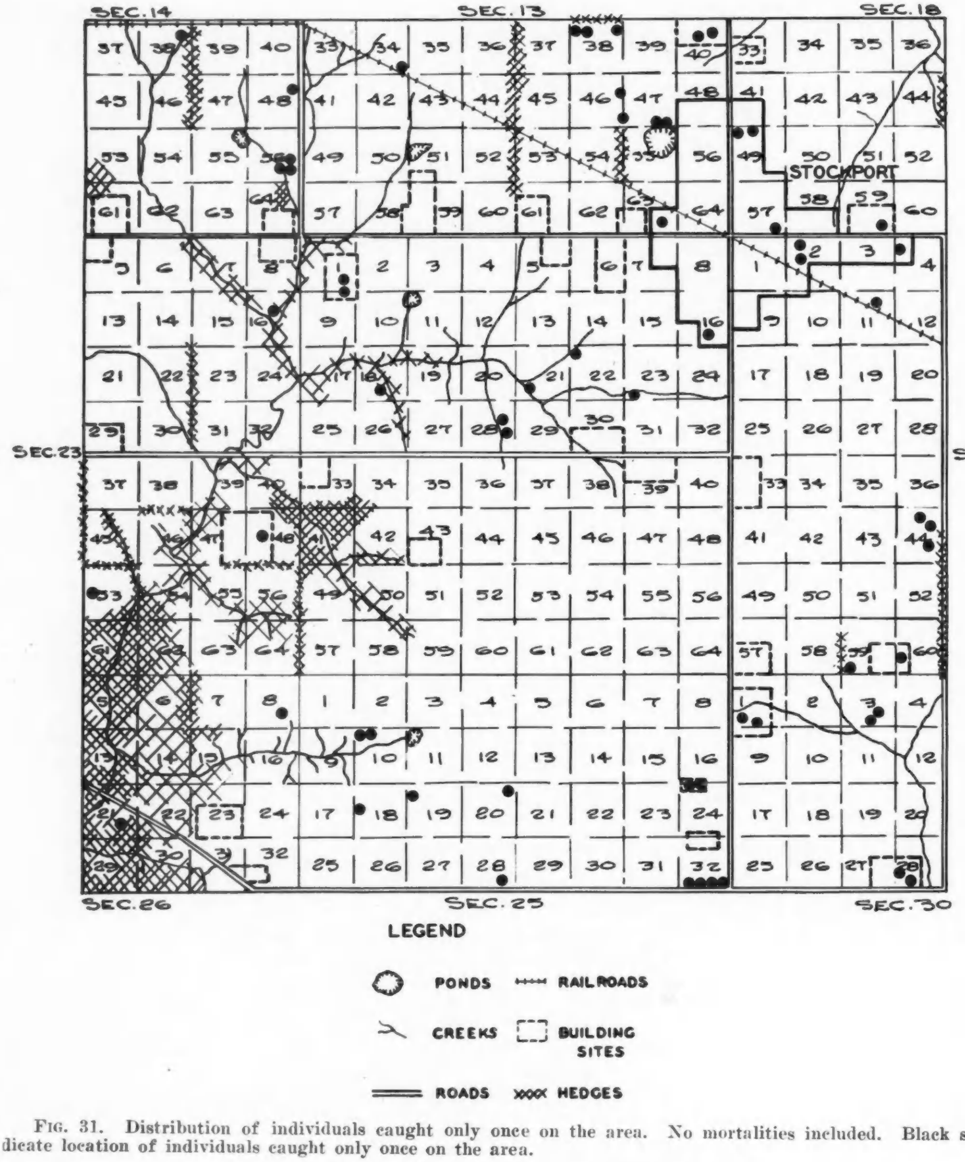

FIG. 31. Distribution of individuals caught only once on the area. No mortalities included. Black spots indicate location of individuals caught only once on the area.

Section	26	25	30	24	18	19	13	14	23
Males	2	8	2	6	3	4	10	2	2
Females	0	4	2	3	1	7	5	2	1

Total 64

(Microtus). From the timothy it recrossed the pasture to a strawpile-butt den, a few rods south of the barn from which it started. At the strawpile den it was caught in one of the box traps. The tracks of the animal were carefully followed all the way. It hunted entirely alone, caught only one mouse (the only feeding sign) and must have been out most of the night for it traveled 4,900 yards or almost three miles, going, hunting and returning. It never got farther than one-third mile from its dens.

During the winter season only one or two records were ever obtained of an animal traveling more than one-half mile and these never exceeded three-fourths of a mile from a central winter den. A skunk's ac-

TABLE 5. Distances traveled by spotted skunks in 24-hour periods.

Date	Place	Observer	Ground Cover	Ground Condition	Travel Distance	Food Procured
1/11/40..	Stockport	Crabb	Short pasture, cornstalks, timothy-hay	10″ packed snow	4,900 yards	Microtus
1/ 5/40..	Stockport	Crabb	Cornstalks, oat stubble, clover field, plowing	½″ snow	3,700 yards	Unknown
7/14/39..	Stockport	Crabb	Weedy fence row	dry	2,640 yards	White grubs in strawpile butts
6/28/39..	Stockport	Crabb	Weedy fence row, field road	dry	200 yards	Phyllophaga under Greater Ragweed
8/15/39..	Stockport	Crabb	Hedge row and weedy fence row	dry	1,100 yards	Wild grapes
6/ 3/39..	Stockport	Crabb	Oatfield 11″ high	dry	880 yards	Pigeon
2/ ?/42..	Stockport	Johnson	Short pasture	2″ snow	220 yards	Unknown
1/15/42..	Stockport	Crabb	Farm yard	18″-24″ new snow	17 yards	None
1/25/39..	Ames	Crabb	Ragweeds and Alfalfa 12″ high	2″ snow	150 yards	Unknown
1/25/39..	Ames	Polderboer	Alfalfa 12″ high	2″ snow	400 yards	Unknown
2/18/39..	Ames	Crabb	Ragweed and Alfalfa 12″ high	4″ melting snow	120 yards	Unknown
2/18/39..	Ames	Crabb, Polderboer	Alfalfa 12″ and sweet clover 18″	4″ melting snow	300 yards	Microtus

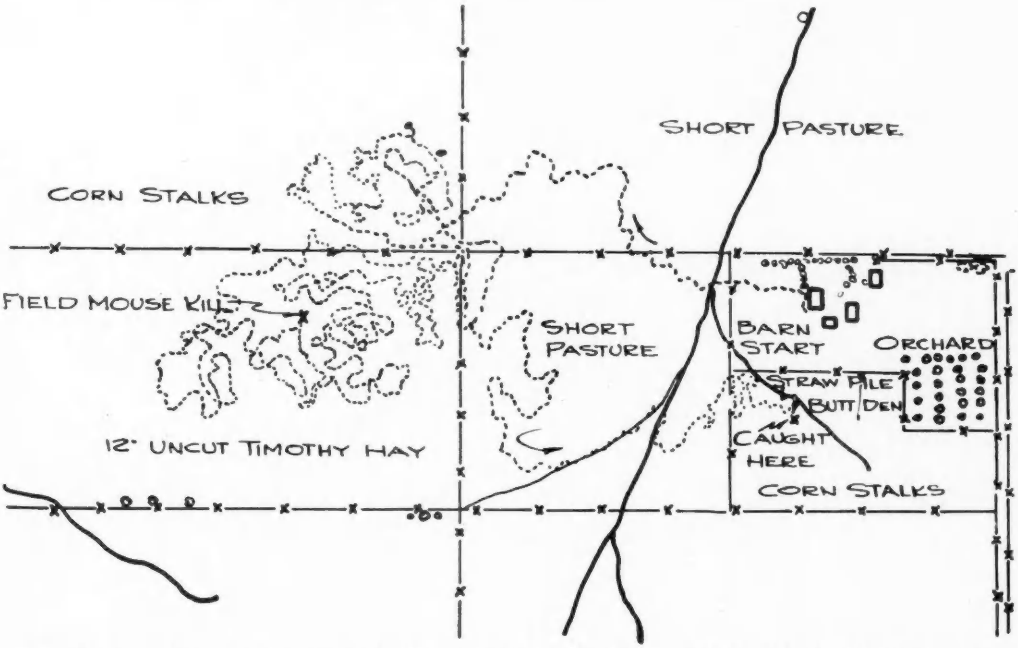

FIG. 32. Ground covered by spotted skunk in one night during January, 1940. Actual distance traveled was 4,900 yards (3 miles). Scale ⅔ in. = 40 rods.

tivity was generally confined to an area of approximately 160 acres.

It is obviously impractical here to describe the case histories of each skunk, but as an example typical of the group the following account is given (Fig. 33, Skunk F):

Jan. 19. Male skunk number A318 was caught beside a shallow open rock wall well, 40 rods south of quadrat 39, section 24, in which there were three winter dens (Fig. 34).

Jan. 21. Caught in southwest corner 20 rods from the dens in quadrat 39.

Jan. 24. Caught in northwest corner of quadrat 39 at a tile opening. On releasing it, it ran to a woodpile across the road in quadrat 30, 20 rods away.

Jan. 26. Caught beside a corncrib den in the farm yard in quadrat 39.

Jan. 31. Caught along fence on east side of quadrat 45, 80 rods southwest of dens in quadrat 39. Trapping on these quadrats was then discontinued until the third week in February.

Feb. 23. Caught on fence line 100 rods southwest of dens in quadrat 39.

Mar. 6. Caught in quadrat 62,120 rods southwest of dens in quadrat 39.

The land over which this male foraged south and west of the den sites was approximately 50% cornstalks, 25% pasture and 25% soy beans and clover stubble.

Females in Winter

Trapped females in winter presented the same or similar activity pattern demonstrated by trapped males. Six individuals were followed by repeated trappings during January and February of 1942. They made similar one-night forays into the surrounding fields during good weather and were to be found in the vicinity of a barn den (5 cases) or a strawpile den (1 case) to which they returned for the day. During wet or very cold weather they remained in their barns entirely. The only evidence of their presence was tracks found on patches of snow drifted through cracks in the barn and by scats or occasional musk.

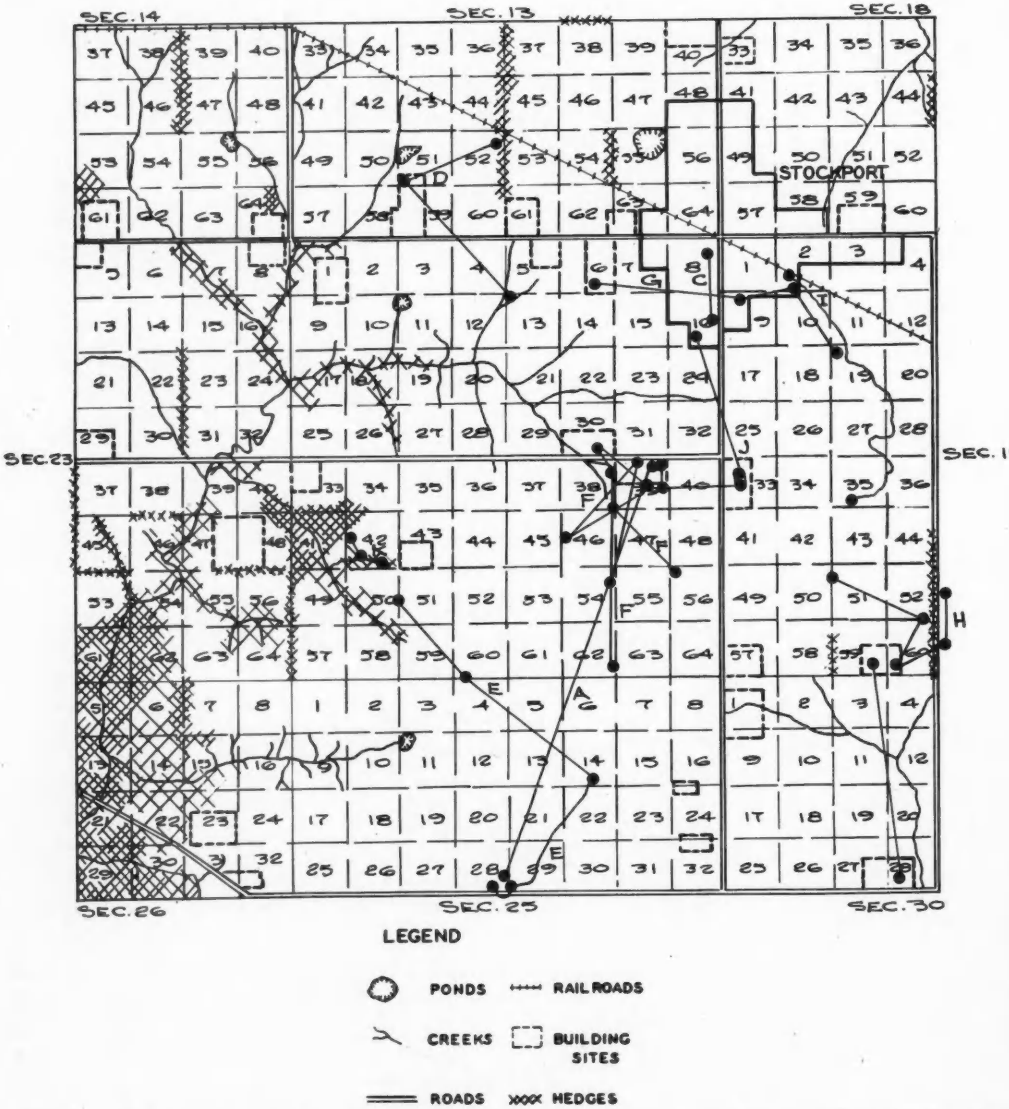

FIG. 33. Males in winter on the area. Only those caught two or more times are represented. Period of movement: Skunk A, Oct. 12-Dec. 6, 1940; skunk B, Dec. 3-9, 1940; skunk C, Dec. 4-7, 1940; skunk D, Jan. 16-Feb. 16, 1942; skunk E, Jan. 17-Feb. 28, 1942; skunk F, Jan. 19-Feb. 23, 1942, skunk G, Jan. 28-Feb. 17, 1942; skunk H, Feb. 5-17, 1942; skunk I, Feb. 11-12, 1942; skunk J, Feb. 16-28, 1942; skunk K, Feb. 23-24, 1942.

FIG. 34. Farm yard, quadrat 39, with several dens used regularly by spotted skunks, winter 1942.

One case history will serve to illustrate the general characteristics of them all (Fig. 36, Skunk G):

Jan. 15, 1942. Female skunk number A314 was captured beside a thrashed clover pile in quadrat 47, section 24. When released she ran down a temporary ground den in a fence line (Fig. 34).

Jan. 21. She was caught at the corncrib den in quadrat 39 (Fig. 35) only eight rods north of the first place.

Jan. 29. Caught at a tile opening at the northwest corner of the same quadrat, about 30 rods away. Trapping was then discontinued until the third week of February.

Feb. 21. Caught in the same quadrat (39) as before but in the barn (Fig. 34).

Feb. 26. Caught at the corner of the chicken house 15 rods west of the barn.

This skunk used the same combination of dens used by skunk number A318 described before but she was not caught much beyond the limits of that one 10-acre quadrat.

Skunks H, F, and B (Fig. 36) were caught at various points in the field as much as 160 rods apart which compares more favorably with male records of this period, but as with males none of the females used more than 160 acres during this season.

Males in Spring

Data on spring activity of males was gathered on 18 individuals using the four sections. Only 10 of these were sufficiently complete to warrant their use in describing activity at this season.

Males at this time of the year traveled about the community. Distances of one-half mile to a mile were regularly traveled between points of capture and at least two of them were caught at points two miles apart during this time (Fig. 37, Skunks P and M). Since two miles was the extent of the area it is not known if they traveled farther. However, six individuals traveled about extensively within the bounds of the four-square-mile area and from these it is assumed that two to four square miles is the probable extent of their "area of familiarity."

The reasons for the extension of ranges beyond that used during the winter were not determined. The search for females in breeding condition was probably an important factor. The availability of considerable insect food in the fields and the habitability of field dens made possible long excursions.

Since the traps were not in every quadrat of the four sections at the time the skunks moved about so extensively only those were caught which traveled in the areas being trapped or into the areas into which

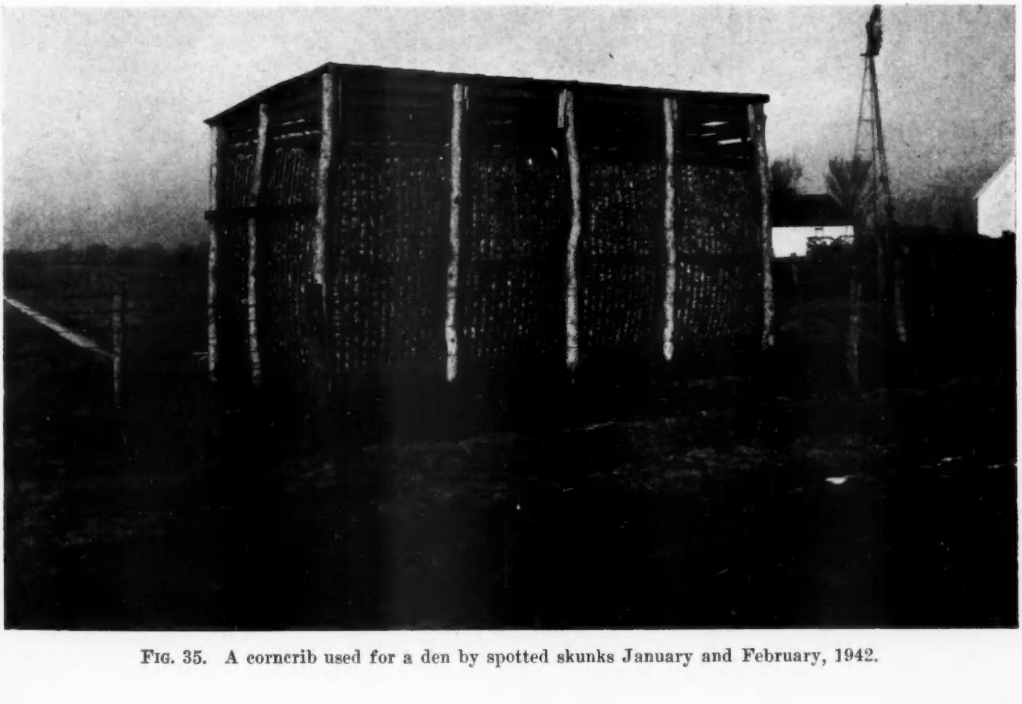

FIG. 35. A corncrib used for a den by spotted skunks January and February, 1942.

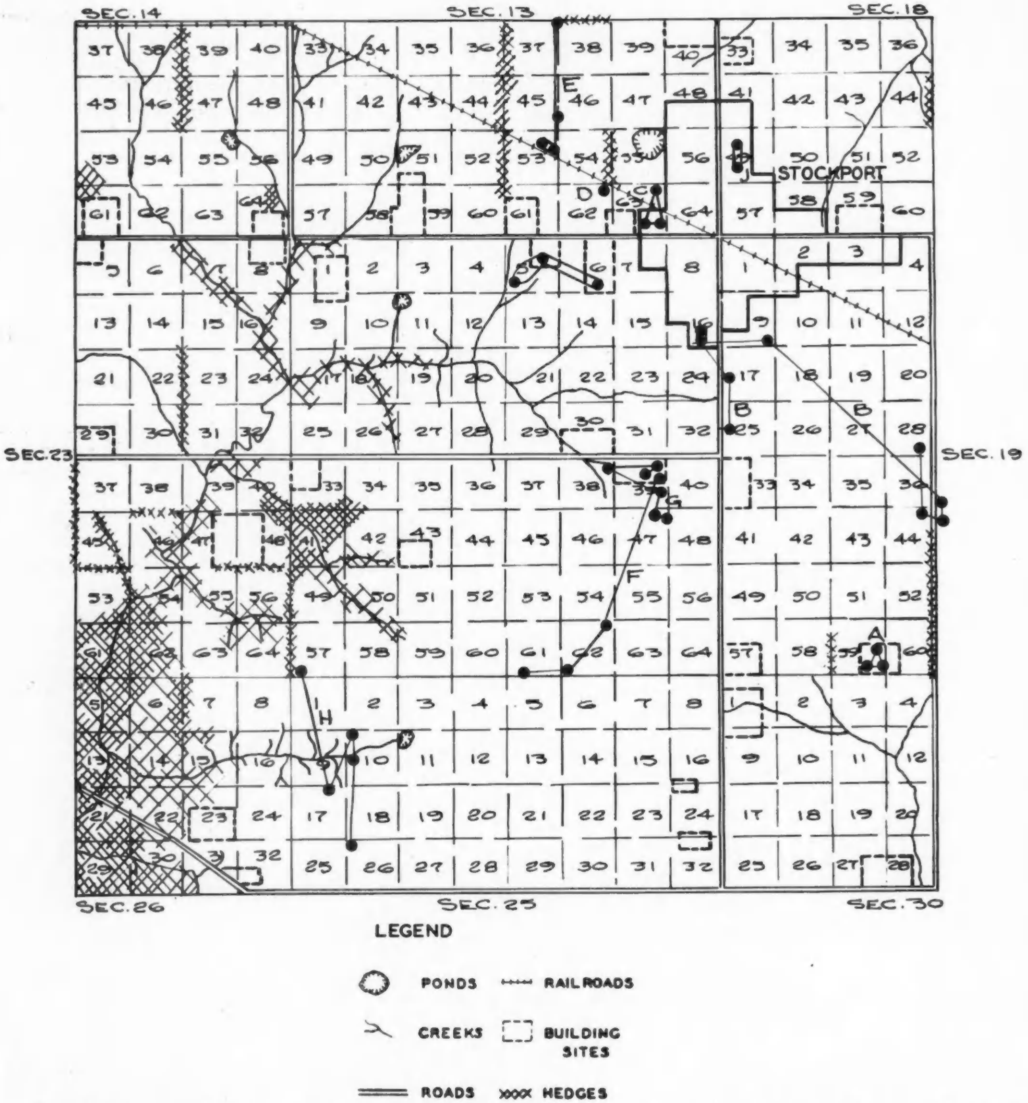

FIG. 36. Females in winter on the area. Only those caught two or more times are represented. Period of movement: Skunk A, Feb. 5-11, 1942; skunk B, Feb. 5-19, 1942; skunk C, Jan. 12-Feb. 16, 1942; skunk D, Feb. 16-March 1, 1942; skunk E, Feb. 2-9, 1942; skunk F, Jan. 16-Feb. 23, 1942; skunk G, Jan. 16-Feb. 26, 1942; skunk H, Jan. 24-Feb. 28, 1942; skunk I, Jan. 30-Feb. 11, 1940; skunk J, Feb. 6-11, 1940.

the traps were later moved. Consequently the extent of coverage of the area by the skunks between the points of capture does not appear on the map. It is believed that the males visited every barn yard and other spotted skunk habitat on the route between the points of capture.

Those skunks on the four sections whose records are of short duration were probably animals whose major activity centered beyond the bounds of the sections trapped. Most of the records concerning them are close to the borders (Fig. 37, Skunks S, T, R, E, Y and W). Almost all of the male skunks at one time or another during this season were trapped close to the borders of the four sections and consequently it is not known if they went beyond them and if so to what extent. Undoubtedly some of them did.

A case history of one male will serve to illustrate the type of activity characteristic of this period:

Feb. 16, 1942. Male skunk number A358 (Fig. 37, Skunk O) was caught by a tree root den on a road bank in quadrat 41, section 13. Its previous history was not known.

Mar. 9. Caught in quadrat 44, section 24 a full mile south and west at a fence corner in an open field.

Mar. 18. Caught in quadrat 22, section 23 three-fourths mile north and west of the second place of capture and one mile southwest of the first place of capture.

Mar. 20. Caught in quadrat 19, section 24 about three-fourths mile directly east of the last above and almost one-half between the first two points.

Mar. 26. Caught in quadrat 39, section 14 about a mile northwest of the place caught on March 20 but only 80 rods from the February point of capture.

Mar. 27. Caught in quadrat 64, section 14 along a road south of the first place about 80 rods.

The traps soon afterwards were moved from this territory and he was not caught again. The known area covered by this male amounted to a little over one and one-fourth square miles.

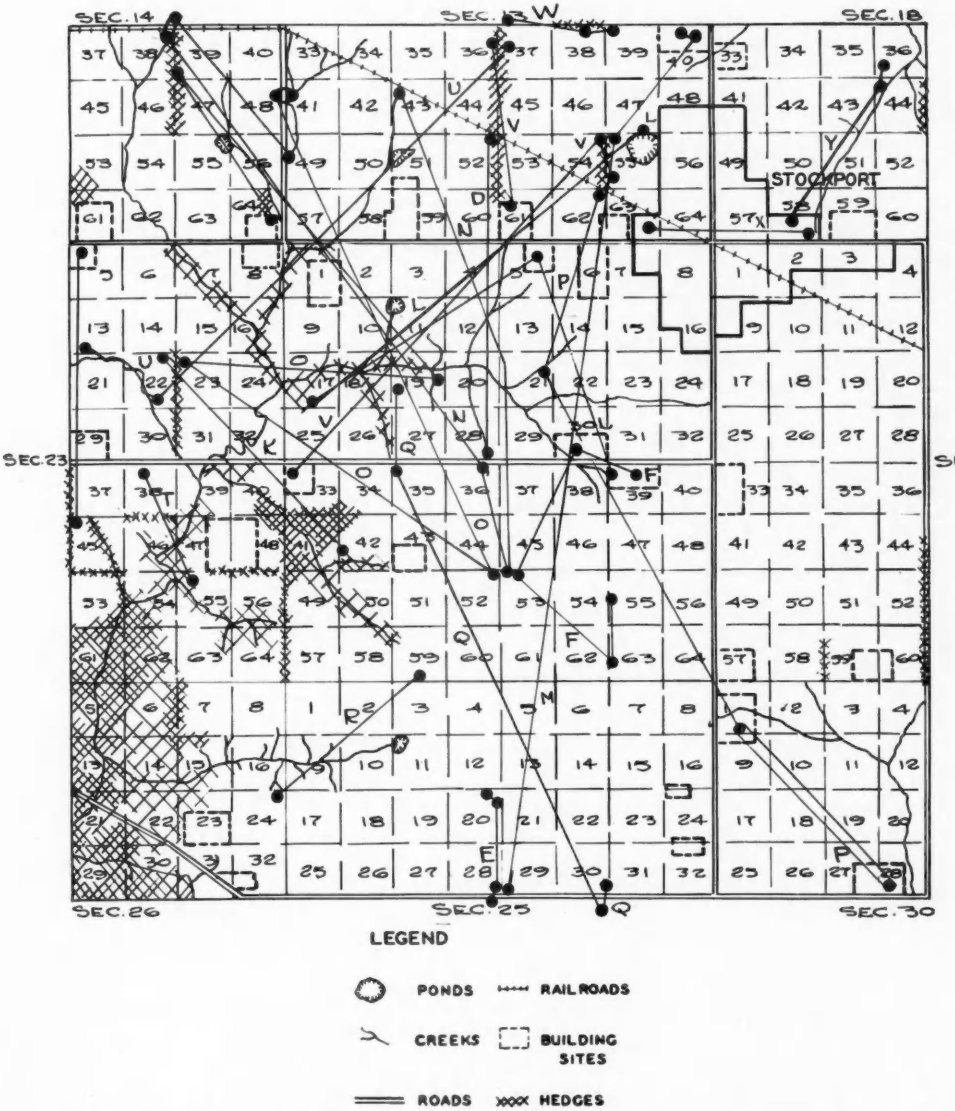

FIG. 37. Males in spring on the area. Only those caught two or more times are represented. Period of movement: Skunk D, Jan. 16-March 17, 1942; skunk E, Jan. 17-March 7, 1942; skunk F, Jan. 19-March 10, 1942; skunk L, Feb. 6-May 6, 1942; skunk M, Feb. 7-June 15, 1942; skunk N, Feb. 16-April 13, 1942; skunk O, Feb. 16-March 27, 1942; skunk P, Feb. 16-24, 1942; skunk K, Jan. 23-March 26, 1942; skunk Q, March 7-26, 1942; skunk R, March 7-25, 1942; skunk S, March 18-April 3, 1942; skunk T, March 23-31, 1942; skunk U, March 26-April 10, 1942; skunk V, April 9-May 18, 1942; skunk W, April 10-11, 1942; skunk X, April 11-12, 1942; skunk Y, April 13-May 1, 1942.

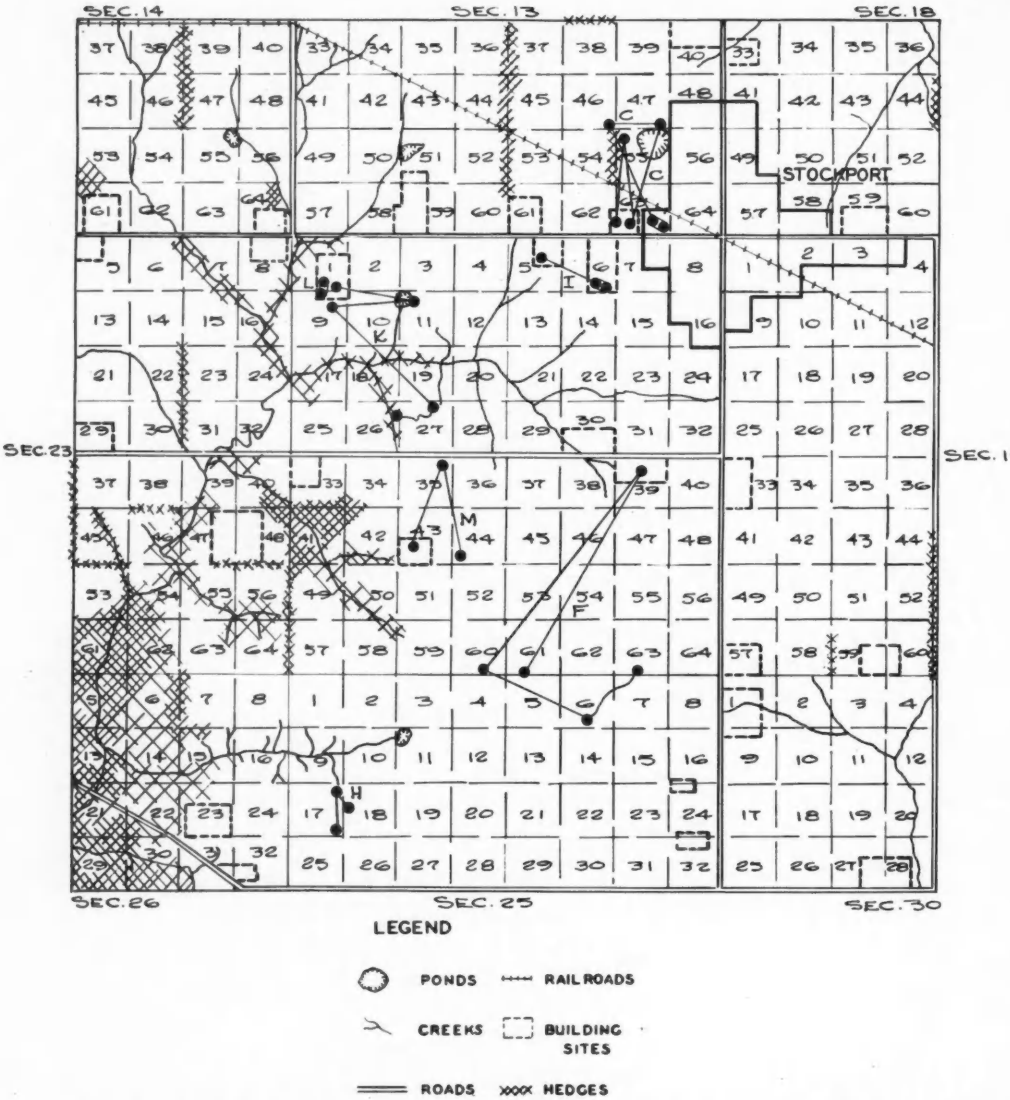

FIG. 38. Females in spring on the area. Only those caught two or more times are represented. Period of movement: Skunk I, Jan. 30-March 14, 1940; skunk C, Jan. 12-May 17, 1942; skunk F, Jan. 16-March 9, 1942; skunk H, Jan. 24-March 7, 1942; skunk K, March 12-April 9, 1942; skunk L, March 13-April 13, 1942; skunk M, March 21-April 25, 1942.

Females in Spring

Although only seven females were trapped frequently enough to use their records for this discussion their ranges were sufficiently uniform to indicate the general activity trend of the sex (Fig. 38).

The extent of their travels is in marked contrast with that of the males at this time of year. While the males were moving all over the community the females changed their travel habits only a little or not at all. None of the cases demonstrated the use of area greater than one-fourth section. However, females seemed difficult to catch during this season and the paucity of data must be considered in evaluating their activities.

One case history, however, is complete for the period and is given in detail here (Fig. 38, Skunk C). This female used 40 acres, quadrats 54, 55, 62, and 63 of section 13 at the northwest edge of the town almost exclusively. She was caught here in January and February but the area was not trapped during March.

April 9. Caught in quadrat 63 behind a chicken house.
April 10. Caught in extreme southeast corner of quadrat 46, 80 rods northwest of the chicken house at the end of a hedge.
April 13. Caught 40 rods east of the latter place above.
April 22. Caught at quadrat 63 beside a hog house, in a farm yard, under which she had a den.
April 24. Caught at same place taken on April 10.
May 10. Caught beside chickenhouse in a steel trap in the farm yard only two rods from her hog house den. The farmer accused her of chicken killing and she was killed.

Males and Females in Summer

Very few data are available on summer activity of either sex. One male caught July 9 in an orchard, near a farm yard was recaught July 23 three-fourths mile south. Two large hay fields, a railroad right-of-way and a long hedge were between the two points. On July 27 he was caught at a farm yard slightly over one mile northeast of the second point and three-fourths mile east of the first point. This animal in three weeks apparently covered about one square mile.

Another male caught within a few yards of the one just described on the same date (July 23) was recaught September 15 one and one-half mile southeast at a farm yard.

Another male traveled one mile between June 6 and June 16. From meager data available very little variation can be seen between spring and summer activity of this sex.

Records of females for the period are also inadequate. Data were gathered on three. Each had a litter of young. None of them were known to leave the vicinity of the maternal den.

Males and Females in Fall

No systematic trapping was done in either summer or fall. Consequently the fall season, too, is poorly represented by mobility data. No female was caught more than once.

Information concerning two males is available for this period. One caught October 12 was followed one-fourth mile to a corncrib den when released and on December 6 it was caught at a well den one mile away from the corncrib and one and one-fourth mile from the point of first capture.

Another male caught October 2 at a barn was recaught the next night 300 yards southwest. On October 5 he was caught one-third mile east of the barn at an abandoned building site (Fig. 23), and on October 19 he was caught in the woods about two-thirds of a mile from the barn towards the southeast. He ran up a tree when released (Fig. 14). The known area used by this animal was less than one-half section.

Juveniles

Approximately 34 juveniles were handled during summer and fall months but only three of them were caught more than once or at sufficient intervals to estimate their movements.

One male caught October 29 at a wood house in town was taken into the country one-third mile. On November 6 he was caught at a chicken house within 100 yards of the wood house. A female caught October 1 in a steel trap lost one front foot and the toes of her other front foot. She was caught several times and her tracks were observed many other times in the vicinity of two farm yards all within an area of 30 acres. She lived under a cob shed all of one winter.

Another male caught August 18, 1941, was recaught March 11, 1942, less than 100 yards from the first place. No other information is available on the animal.

SUSCEPTIBILITY TO TRANSPLANTATION

Transplanting or moving spotted skunks has been attempted by farmers and others as a management practice. Removal of skunks from a dwelling because they are a nuisance, or moving them to barns for rat control, is sometimes desired. Some data were gathered concerning this type of management and its results.

During March, 1942, three male and three female spotted skunks were caught in live traps outside of the study area and moved a minimum of two miles and a maximum of three miles into the center of the four sections under intensive trapping. They were released in farm yards that no other spotted skunks were known to be using, although at one place where a male and female were released a dog had killed a female six weeks earlier. Both places were regularly used by spotted skunks in other years and generally appeared to be excellent habitats. Both places were soon afterwards trapped by the quadrat system for at least three weeks.

None of the males ever appeared in the traps at the point of release or within a mile of that point. Evidently they immediately left the four-section area. One of the females also never was retaken, but two of the females were caught again. These were released a day apart (March 12 and 13) each with one of the males just mentioned in the same barn. One of the females was caught in a field six days after release within 40 rods of the barn where she was turned loose. Three weeks later on April 9 she was caught again about 80 rods south of the barn but only 20 rods southwest of another barn on the same farm. She evidently had adjusted herself to the new location. The other female released at this place was caught April 13, exactly one month later, within 50 yards of the barn in which she was released. She ran into a pile of logs where she had a den in a hollow of one of the largest. Both animals were in excellent condition. One had gained an ounce and the other two ounces. However, they may have been pregnant.

Frequently requests were made by farmers that spotted skunks be caught and removed, especially where they were inhabiting a house. This was done on several occasions to keep the goodwill of the farmers. In keeping with the plans of the investigation, to have a minimum amount of effect upon natural behavior, they were ordinarily released less than a mile away and if possible well within the animal's

probable area of familiarity. This, of course, did not solve the farmer's problem for the transported skunk either quickly found its way back or others came in unless the den entrances were carefully blocked. Intensive trapping was not practiced over long periods when most of the animals were moved, so little opportunity was afforded for checking the return of trapped and transported individuals.

One male caught April 10 at a farm house on the area was moved one and one-half miles away to the southwest; on April 13 it was caught again 80 rods northeast of the house from which it was first taken. This animal lost no time in returning nearly two miles to the vicinity of the former den.

Another male trapped by a steel trap in a wood shed in town was taken three-fourths mile away on October 29. One leg was broken and bleeding. On November 6, one week later, it was recaught within 100 yards of the wood shed beside a hollow tile chicken house where it probably had a den.

Several other animals were moved in a like manner and were never recaught. That fact, however, may have been due to a cessation of trapping and not to the transplanting.

Considerable more data will need to be gathered on this type of behavior before either transplanting or removing can be recommended as a worthwhile management practice.

Susceptibility to Domestication

Animals with beneficial food habits, valuable hides, or some other attributes have been domesticated by man since the dawn of history. The domestication of fur-bearing animals for their product is a comparatively recent practice yet it has now reached the stage were fur-farming of fox and mink is an important branch of animal husbandry. While the spotted skunks may never become important as a domesticated animal a few remarks about its susceptibility to domestication may not be out of place.

While investigating various phases of the general spotted skunk problem it has been expedient from time to time to have one or more of the animals in captivity.

Late in the fall, 1938, a wild adult female was caught uninjured and kept throughout the winter and spring for observation of eating habits, food capacity, appearance of scats and study of disposition. This animal was kept in a wire cloth cage of one-half inch mesh, two feet by three feet, and with a small nest box in one end. From the first day she ate readily almost anything edible put in the cage. The appearance of her scats was used as an indicator of her general well-being and the food was varied when the scats appeared to vary from "normal."

She was turned loose seven months later apparently none the worse for her experience. She never used her musk while in captivity.

Three litters of young have been raised in captivity, one of them from birth (Crabb 1944). They were easily raised on a diet of pigeon *(Columba livia)*, commercial dogfood, corn, and miscellaneous fruits.

Skunks have cleanly habits, and usually use a corner of the feed pen for defecation. They seemed loath to come out of a tight nest box during the day, if the feeding pen was in a brightly lighted place, and would defecate in a corner of the nest box if it was large enough so that they are not forced to sleep on their scats.

Wild animals taken into captivity for two or three days for observation invariably ate food put before them as soon as they became hungry. They ordinarily made an effort to escape and would work their way out of anything but the most carefully constructed cage. No attempts were made to breed them in captivity but it probably could be done successfully.

The individuals kept in captivity varied considerably in disposition. Some of the young raised were quite gentle while others were unfriendly and even vicious. They all resented handling and when full grown would not allow themselves to be touched. They showed little inclinations to musk for they were not afraid but they were quick to bite and in an impudent and threatening manner kept their caretaker at a safe distance. The young in captivity seemed to get along well together and had no fights even when full grown. They played rugged wrestling games with one another, stamped their feet and threatened with their tails in a most serious manner, but their threats were not taken seriously. Many of their antics were very similar to those of kittens of a like age.

Mortality

Even though the spotted skunk has remarkable abilities to take care of itself when in difficult situations, by habitually living about farm yards in southeast Iowa it subjects itself to some severe decimating potentials, especially dogs and men.

During the course of this investigation of 39 months during which 24 months were spent in residence on the area, records were obtained on the deaths of 77 spotted skunks. Undoubtedly there were others for only such records were obtained during the time away from the area as farmers remembered with sufficient accuracy to report. Even when the investigator was on the area farmers would frequently forget or neglect to mention the killing of one of the skunks.

Besides the accidental or deliberate killing by farmers, undoubtedly other skunks died from natural causes in places that they were never found. Unlike most species of wildlife, however, a dead skunk usually leave a memorial to itself for two or three months in the form of the rotting scent glands. By one's nose remains of the carcass may be located weeks or even months afterwards when it is under a building or in another protecting situation.

Of the 77 spotted skunks known to have died on the area 25 skunks of 32.47% were trapped for fur. Almost all of these were trapped by three boys in one family who were the only regular fur-trappers on the area. They seldom set traps for the animal but usually caught it in traps placed for mink and striped skunk. They did not feel well paid for their

troubles since twenty-five or thirty cents was the price of a prime spotted skunk pelt during the period of study.

Twenty-one skunks of 27.27% were killed by farmers for suspected or proven predation on chickens or because their odor was a nuisance about the buildings (Fig. 39). Twenty skunks or 25.98% were killed by dogs. Man was often an accessory to the dog-killing. He may have purposely exposed the spotted skunk by moving boards or baled straw after the dog had "treed" the animal. By his help and approval of such activities some dogs constantly worked the premises in search of the spotted skunks. Together these two decimating methods account for 53.27% of the total mortality known on the area (Table 6).

FIG. 39. A chicken killed by spotted skunk February, 1942. Note mutilation of head and neck.

TABLE 6. Classification of Mortality on Stockport Area.

Number	Class	Percent
25	Fur	32.47
21	Nuisance	27.27
20	Dogs	25.98
3	Traffic	3.89
3	Malice	3.89
2	Cats	2.59
3	Unknown	3.89
77		99.98

Three were killed by highway traffic on the area (Fig 40). Spotted skunks are frequently killed on highways in Iowa. Records were not kept on this type of mortality except on one occasion when dead skunks seemed to be especially numerous. On a round trip of 595 miles between Stockport and Sioux City, Iowa, during the last week of April, 1942, 19 dead spotted skunks were seen on the road for an average of almost one every 26 miles. The route was retraced only 100 miles. Five of the skunks were counted on an 11-mile stretch of pavement between Ames and Boone in the center of the state.

Two skunks were killed by cats, three were killed for no good reason by man, and three died from unknown causes on the area. The last three were discovered by the "nose" method mentioned above sometime after it was too late to detect violence other than broken bones.

The two spotted skunks killed by cats were not seen by the writer for the farmer failed to report the

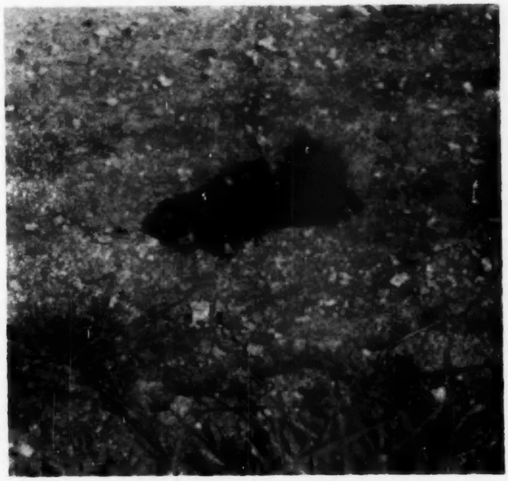

FIG. 40. Juvenile spotted skunk killed by traffic August 10, 1939 on the area.

incident until three or four days after they happened. The farmer's story is believed to be true. It is as follows: He had five cats of the common kind found about Iowa farm yards. These cats were regularly being polluted by spotted skunks that had a den in the hay stored in the cow barn. The fact that they often smelled of skunk indicated that they were fighting or molesting the skunks regularly. The first week in April, 1942, two of these cats dragged a freshly killed and highly smelling skunk in behind the cows and began to eat it while the farmer milked in the evening. He promptly removed them from the barn. The three other cats joined the first two and they ate the spotted skunk while the farmer looked on. The next night the incident was repeated with another spotted skunk in almost the same manner.

Although great horned owls were resident on the area throughout the course of this investigation no evidence of skunk predation was ever seen in their pellets. Errington (1940 and in conversation) expressed the opinion that skunks were quite common in the diet of this owl in proportion to their population densities.

An attempt to catalogue farmer attitude toward the spotted skunk on the area was made during May of 1942. Seventy-seven farmers were seen. Of this number 85% had had these little skunks about their buildings in the past year and knew they were there. The other 15% did not know of any on their places or were not sure. Thirty-four percent said they had trouble of one kind or another with skunks. The trouble consisted largely of predation on chickens or egg eating, and as a nuisance, such as living about houses and stinking up the premises. Sixty-six percent had no trouble or did not know about it. Twenty-one percent attempted to manage the spotted skunks about their farms by trapping, poisoning, or blocking them out of their dens, such as plugging holes in

foundations or placing moth balls in the entrances. This figure represents about two-thirds of those that had trouble with spotted skunks. As an indication of farmer attitude towards the spotted skunks 19% of the 77 farmers were definitely against having them on the premises and practiced their destruction at every opportunity. These 19% were largely responsible for 50% of the mortality as listed under dogs and men. Twenty-eight percent of the farmers were glad to have them tended to encourage them whenever possible. Fifty percent of the farmers were indifferent or apathetic towards them.

Mortality on the Stockport area was greatest during the winter months (32.66%) and least during the summer months (15.62%). Fall trapping probably contributes to a rather high mortality rate during that season (28.40%). However, these data are hardly adequate to be significant and are only presented to suggest general trends (Fig. 41).

Defense and Offense

The spotted skunk is remarkably well equipped for self defense. The liquid musk common to all mustelids is a potent weapon of defense with this species. It is secreted by two glands located on either side of the tail and is stored for use in vesicles with a capacity of about one tablespoon each (Blackman 1911). The active ingredient of the musk is a sulphide called mercaptan. The fluid is discharged through nipples hidden within the anus when the tail is down but which are protruded when the tail is raised over the back. The use of the musk is a last resort in defense.

The skunks handled in the traps usually gave several definite warning signals before using their stink. Stamping or patting the front feet in rapid succession on the floor or ground can plainly be heard for several feet. But this warning may be of two kinds: (1) it may be an indication of anger, the threat carried out by biting and snarling especially when directed toward one of their own species; (2) it may indicate fright which is always accompanied by raising the tail and discharging the musk unless the bluff is effective and the skunk begins to feel secure.

Another common warning of anger and fear is the use of the "hand-stand" (Johnson 1921, and others). The writer has seen spotted skunks walk several yards on their front feet with their tails high in the air. They frequently do not discharge scent when performing this antic but will if too closely pressed. The author has seen the "hand-stand" performed when a skunk was too closely pursued by inquisitive pigs after being released from a trap. In this instance one pig came too close and received a small discharge of the musk on his face. At times the "hand-stand" is used as a playful gesture (Walker 1930). The writer has seen half-grown spotted skunks do it when playing among themselves.

Although it is generally believed that this skunk cannot discharge its odor with the tail down the notion is only partially true. When securely pressed into the tagging chute they are unable to lift the tail above their backs but by swinging it sideways they expose the anal sphincter. When thoroughly frightened the animal musks even if the offensive fluid is discharged all over the tail. Normally the tail is lifted to clear the "line of fire" and as a warning as much as a method of preparation.

On a still day the musk can be discharged five or six feet with deadly accuracy. On a windy day one can feel the spray on the face as far as two or three rods if he is unfortunate enough to be standing downwind.

The anal fluid when seen macroscopically appears much like skim milk with some curds of cream mixed with it. The basic color varies from white through light yellow to greenish yellow but almost always the white curds appear.

The climbing of trees or fence posts is a preferred method of defense against dogs and men. While they do not appear as adept in the trees as squirrels yet they climb rapidly and will stay secure in a high crotch all day if danger below continues to threaten (Fig 13).

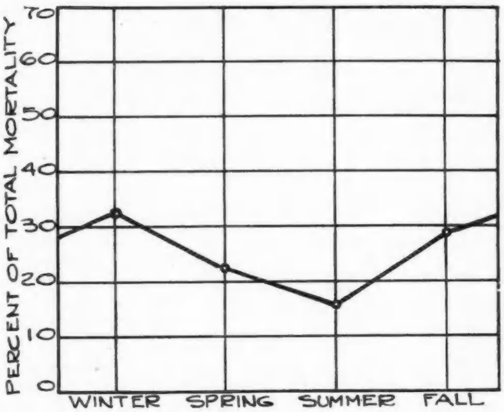

FIG. 41. Percent of total mortality on the Stockport area by seasons.

MANAGEMENT OF SPOTTED SKUNKS

Management of spotted skunks within the Stockport area embraces two opposing aspects, namely encouragement and discouragement. As with many other wildlife species the decision to do one or the other often rests upon a very delicate balance.

No particular attempts at management were made during the course of this investigation. However, for many farmers on the area, management of the spotted skunk was often a very pressing problem. Almost all farmers practiced one form or another at various times whether consciously or otherwise.

After four years of study of the food habits, life history and ecology of the species only a few questions can be answered with certainty. The decision whether to encourage or discourage the animal must still be determined by considering individual circumstances and particular situations. This is a most important fact. Many farmers unequivocally classify such animals as the spotted skunk as "vermin" on

the basis of a violated hen roost sometime several years before and kill the spotted skunks on circumstantial evidence or for no satisfactory reason.

It was shown in the food habits investigation (Crabb 1941) that the bulk of food consumed by these skunks was to the farmer's benefit or at least not detrimental to his interests. On a basis of 834 analyzed scats from every season less than 1.5% were found to contain poultry remains, but almost all of the chicken eaten was carrion. During winter and spring months rats and mice remains appeared in 40 percent of the scats. During summer and fall food consumed was largely insects and fruits of no particular economic importance one way or another. Even though rats and mice were left unmolested during the warmer seasons these skunks ought to be spared as possible potential allies of the farmer in rodent control.

As was pointed out in the section on habitat the choice of a house or other establishment for a den is often dependent upon the presence of certain foods and often the skunk is feeding on resident rats and mice—a good work—while he is otherwise unwelcome. It was observed a number of times in the winter and spring of 1939, when a heavy population of rats was common all over southern Iowa, that the only buildings accessible to rats and not overrun by them were those used as dens by spotted skunks. In similar circumstances good cats and dogs seemed to have no effect upon the rats and mice. It must be remarked, however, that buildings sometimes within 30 yards of a den building would at the same time be overrun with the rodents.

It is becoming increasingly apparent from the work of Errington, Hamerstrom, & Hamerstrom (1940) and Errington (1942) and others who have studied the intricate relationships existing between predator and prey populations that predators seldom have the controlling or depressing effect upon prey populations that has been so freely credited to them by many observers. The whole problem of rodent control about Iowa farms by spotted skunks needs careful investigation from this point of view.

Many farmers favor the spotted skunks about their farms. They encourage them by restraining the dog from their pursuit, by permitting strawpiles used for dens to stand and rot down, by releasing them when they are caught in traps set for rats, by refraining from trapping them for fur when they are of little value and by letting the skunk go on his way unmolested when they chance to meet. As was pointed out in the section on mortality approximately 50% of the total number killed on the area was killed by farm dogs and farmers with adverse attitudes. It seems then, that the most profitable results in "encouragement" management might come from a thorough educational campaign based upon what is known of the animal's daily life.

Management of the "discouragement" type under some circumstances undoubtedly is necessary. Skunks frequently make dens in houses, wells, and among stored feed where their presence is not conducive to human well-being if not actually detrimental to human health.

Certain individuals, like individuals of many other species, even the domestic dog, cat or hog, may learn to kill and eat chickens and in these cases about the only way to break the habit is to destroy the offender. Chicken, when once its acquaintance is made is well liked by the spotted skunk as well as many others.

When spotted skunks must be removed from buildings they may be easily trapped in box traps and if kept in a dark box may be moved any distance without fear of offensive odor. They may be killed, but most important is the removal of the temptation to return. As was stated in the sections on transplanting and habitats unless the habitat is altered the same skunks or other skunks soon come to occupy the dens. The holes must be destroyed or blocked and tempting food must be removed or placed beyond reach if spotted skunks are to be kept away.

In summarizing management ideas it can be said that many of the same principles that apply to good farming apply to good spotted skunk management. Eggs should be gathered regularly; dead chickens should be buried; farm yards should be kept reasonably clean; and houses, chicken houses and other buildings should be constructed to discourage their use by harmful rodents. These things are conducive to the well-being of both the livestock and the farmer.

In the light of present knowledge the spotted skunk should be condemned only on direct evidence. It should be encouraged about those buildings where rats and mice are prevalent and a little odor occasionally is not objectionable. Many good farming practices are the best insurance against unfortunate experiences with this species.

SUMMARY

The prairie spotted skunk (*Spilogale interrupta* Rafinesque) was studied individually and as a population on 17.5-section area in southeast Iowa during 39 months from March, 1939, to June, 1942, in which 24 months were spent in residence on the area. The area is comprised of approximately 7.5 sections of woodland pasture and 10 sections of flat intensively cultivated agricultural land. There are approximately 78 farmers and sites of farm buildings on the area. The farms average 145 acres.

Techniques employed in the field are described. They deal largely with a system of trapping and eartagging the spotted skunk. Signs such as tracks, scats, dens, and evidence of feeding are described.

Spotted skunk habitat was characterized by a large number of dens distributed over the range. These dens were not the property of one skunk but of the population. The living space of individual skunks at any one time included several dens, available food, and safe passage between dens and food. Spotted skunk dens were largely located in and about farm yards. Very few ground dens were used. Those used were appropriated from other species. There were 5.3 farm yards per section with an average of 13 semi-permanent or permanent den sites.

The population was trapped intensely during the winter and spring of 1942 on four sections in the center of the area. The population density was determined at 13 spotted skunks per square mile in late winter and early spring of 1942. The sex ratio was 1.68:1 on a basis of 74 males and 44 females.

The living space of individuals was found to be similar for males and females during the winter season. One quarter section with two or three dens contained the average individual. The living space of individual females in spring was approximately the same as that during the winter months. The living space of individual males during the spring was found to be greatly expanded over that used during the winter. They used two to four sections each. Individuals traveled from a few yards to several miles on feeding trips during winter time but seldom got more than one-fourth mile from the central den.

Spotted skunks were easily kept in captivity, but were not particularly easy to tame.

Seventy-seven spotted skunks were killed on the area: 32% for fur and 53% for being a nuisance or for predation on poultry. Mortality was greatest during winter and least during the summer. Eighty-five percent of the farmers on the area had had the spotted skunks about their farm yards during the period from June, 1941, to June, 1942. Thirty-four percent had had trouble with them. Twenty-one percent attempted to manage them. Twenty-eight percent encouraged their presence about the premises, 19% were definitely against having them about their premises, and 50% were apathetic toward them.

Of six spotted skunks transplanted to new areas two transplants were known to have been successful.

Wise management of spotted skunks is coordinated with many good farming practices. In general spotted skunks deserve encouragement about Iowa farms.

LITERATURE CITED

Bennitt, Rudolf, & Werner O. Nagel. 1937 A survey of the resident game and fur-bearers of Missouri. Univ. of Missouri Studies **12:** 122.

Blackman, M. W. 1911. The anal glands of Mephitis mephitica. Anat. Rec. **5:** 491-504.

Burt, William Henry. 1940. Territorial behavior and populations of some small mammals in southern Michigan. Misc. Publ. Mus. Zool., Univ. Mich. **45:** 37.

Crabb, Wilfred D. 1939. Abundance of the Upland Plover in Van Buren County. Iowa Bird Life **9:** 41.

1941. Food habits of the prairie spotted skunk in southeastern Iowa. Journ. Mammal. **22:** 349-364.

1941a. A technique for trapping and tagging spotted skunks. Journ. Wildlife Manag. **5:** 371-374.

1944. Growth, development and seasonal weights of spotted skunks. Journ. Mammal. **25:** 213-221.

Errington, Paul L. 1939. Suggestions for appraising effects of predation on local areas managed for bobwhite. Trans. Fourth Wildlife Confer. Amer. Wildlife Inst., Washington, D. C.: 425.

1942. An analysis of mink predation upon muskrats in north-central United States. Unpublished manuscript, Iowa State College.

Errington, Paul L., Frances Hamerstrom, & F. N. Hamerstrom, Jr. 1940. The great horned owl and its prey in north-central United States. Iowa Agr. Exp. Sta. Res. Bul. **27:** p. 793.

Genaux, Charles M., & John G. Kuenzel. 1939. Defects which reduce quality and yield of oak-hickory stand in southeastern Iowa. Iowa Agr. Exp. Sta. Res. Bul. 269.

Hendrickson, Geo. O. 1939. Inventory methods for mearns cottontail. Trans. Fourth Wildlife Confer. Amer. Wildlife Inst., Washington, D. C.: 209-215.

1941. Studies with cottontail rabbit, Sylvilagus floridanus mearnsii (Allen). Quart. Re. for Jan., Feb., and March, 1941, Iowa Coop. Wildlife Res. Unit, Iowa State Col., Ames, Iowa: 23.

Johnson, Charles Eugene. 1921. The "hand-stand" habit of the spotted skunk. Journ. Mammal. **2:** 87-89.

Lantz, D. E. 1905. Kansas Mammals in their relation to agriculture. Kansas Agr. Exp. Sta. Bul. **129:** 390.

Nice, Margaret Morse. 1941. The role of territory in bird life. Amer. Midl. Nat. **26:** 441-487.

Pellett, Frank C. 1913. Food habits of the skunk. Proc. Iowa Acad. Sci. **20:** 307-309.

Reed, Charles D. 1938-1941. Monthly Reports. U. S. Dept. Agr. Weather Bur., Iowa Sect. **50:** 1-124, **51:** 1-126, **52:** 1-124.

Scott, Thos. G. 1943. Some food coactions of the northern plains red fox. Ecol. Monogr. **13:** 427-479.

1937. Mammals of Iowa. Iowa State Col. Jour. Sci. **12:** 43-97.

Seton, E. T. 1937. Lives of the game animals. Lit. Guild Amer. Inc., New York. **2:** 384-401.

Stevenson, W. H. et al. 1918. Soil survey of Iowa, Van Buren County. Soil Survey Report No. &, Iowa Agr. Exp. Sta., Iowa State College, Ames, Iowa.

Walker, Alex. 1930. The "hand-stand" and some other habits of the Oregon spotted skunk. Jour. Mammal. **11:** 227-229.

THE DISTRIBUTION OF LARGER PLANKTONIC CRUSTACEA ON GEORGES BANK

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THE DISTRIBUTION OF LARGER PLANKTONIC CRUSTACEA ON GEORGES BANK

INTRODUCTION

Factors contributing to the productivity of Georges Bank, an extensive and important fishing area east of Cape Cod, were investigated from September 1939 to June 1941. Stations occupied and general hydrographic conditions that existed during the eleven cruises have already been described (Clarke, Pierce, & Bumpus 1943). The present paper now discusses the plankton collections made by the 1.5 meter stramin net with special reference to the larger Crustacea such as amphipods, euphausiids, mysids and decapods.

A number of investigators (Smith & Verril 1873; Bigelow 1926; Needler 1930) have found that with the possible exception of the bottom feeding haddock several commercially important fish of Georges Bank, such as mackerel, herring, and even cod, though perhaps to a lesser extent than the others, depend on the larger Crustacea or their larvae for much of their food. Hence the larger Crustacea can be considered important in the food cycle of Georges Bank.

Excepting the cruise of January, 1940, these larger Crustacea constituted more than half the volume of the stramin net hauls in 60% to 80% of the cases for each cruise. This volumetric abundance of the plankton is presently described. Species composition of the larger Crustacea, the occurrence of predominating species, and effects of the physical factors on distribution are also presented and the results analyzed.

I am greatly indebted to the Woods Hole Oceanographic Institution for making this investigation possible, and take great pleasure in thanking Dr. George L. Clarke for his unfailing interest and helpful counsel. I am also indebted to Dr. Alfred C. Redfield for criticism of the manuscript. Acknowledgment of courtesies is also due Dr. C. R. Shoemaker and Dr. W. L. Schmitt of the National Museum for assistance in the identification of several species and to Mr. Dean F. Bumpus of the Woods Hole Oceanographic Institution, who supervised the collection of the plankton on Georges Bank and examined the plankton sampler tows.

COLLECTION AND ANALYSIS OF DATA

A stramin net (diameter: 1.5 m., mesh 6 strands per cm.) with a 1.0 m. No. 00 silk inner tail (11 strands/cm.) was used. An outside ring, to which was fitted wooden rollers, was attached to the net ring in order that the net could be safely towed as deeply as possible without fouling if it should strike bottom. The net was lowered until its edge touched bottom or, as in deep water beyond the edge of the bank, to a maximum depth of 200 meters. It was subsequently raised so as to make an oblique tow of from 30 minutes to 80 minutes. The steps by which the net was raised were as follows:

At stations with depth of 35-50m. net was raised 5 m. every 4 minutes.
At stations with depth of 50-75 m. net was raised 5 m. every 3 minutes.
At stations with depth of 75-100 m. net was raised 5 m. every 2 minutes.
At stations with depth of 100-150 m. net was raised 5 m. every 1.5 minutes.
At stations with depth of 150-200 m. net was raised 5 m. every 1.0 minutes.

Data which would represent the whole area as accurately as possible were obtained by covering Georges Bank with a net-work of stations 10-20 miles apart. The towing speed for the stramin net hauls averaged 2 knots or 61.7 meters per minute. On this basis the linear extent of a tow of 30 minutes would be 1851 meters or about a mile. Since duration of the tows varied, results were expressed by the number of individuals per 1000 revolutions of a flow meter which was fitted in the mouth of the net to determine the relative amount of water passing through. Hauls reduced to this basis are termed standard hauls in the present report.

By the use of the flow meter it is possible to express results on a relatively quantitative basis even though speed of the ship unavoidably varied and the net probably clogged to different degrees under different conditions. Nevertheless, the actual amount of water filtered during the standard haul is not known because of water lost owing to backwash from the mouth of the net. An approximate value may be reached, however, by comparison with the number of organisms caught at the same stations by Clarke plankton samplers (Clarke & Bumpus 1940) for which the volume of water filtered is accurately known, since each instrument is provided with a propeller geared to a cyclometer which thus measures the volume of water that has passed through the net. Since the plankton samplers rarely caught large numbers of the crustaceans taken by the stramin net, conversion factors were obtained from another part of the investigation where ample numbers of fish larvae were taken in nets of both types.

Use of these factors showed that the amount of water actually passing through the stramin net during 1000 revolutions of the flow meter varied between 150 and 500 cubic meters or had an approximate average volume of 300 cubic meters. This variation was apparently due to difference in meters used from

cruise to cruise and in the exact orientation of the meter in relation to water passing through the net.

These volumes may be compared with the theoretical amount which would result if all water was filtered by the stramin net towed for 30 minutes at 2 knots. The volume of the cylinder 1851 meters in length and 1.5 meters in diameter would be 3258 m^3. The average number of revolutions for a 30 minute tow has been found to reach 3600. Hence the maximum value corresponding to 1000 revolutions of the flow meter would be 905 $m.^3$ for 100% filtering efficiency. Since the values obtained from the fish larvae study showed that between 150 and 500 $m.^3$ were actually filtered, a working efficiency of the stramin net of between 16% and 55% may be obtained.

One thus has an approximate idea of the amount of water filtered by the standard stramin haul. It is unfortunate that there may have been a threefold variation in this value but since in most cases the abundance of the plankton varies by a much greater amount, the results can be regarded as being on a quantitative basis.

For each station, either the whole sample or several parts, each not less than 10%, of the sample were examined. All amphipods, mysids, euphausiids, and decapods in the plankton were identified and counted and the number per standard haul was calculated.

Since vertical distribution of the larger Crustacea is not readily determined by stramin net, Clarke plankton samplers were used to provide these data. The sampler is equipped with a shutter, hence while being towed, its mouth can be opened or closed. In this way a single instrument can be used to sample separate levels of the water column, one at a time, or a series of samplers to be opened and closed at desired depths can be towed simultaneously. The terms "Shallow," "Second-depth" and "Deep," introduced by Clarke, Pierce, & Bumpus (1943), will describe the strata fished by the plankton samplers when vertical distribution of the Crustacea is discussed. The depths of the water that corresponded to the strata were as follows:

Stratum	*Water less than 75 m.*	*Water more than 75 m.*
"Shallow"	0 m. to 25 m.	0 m. to 25 m.
"Second-depth"	25 m. to bottom	25 m. to half-distance to bottom (or to half-distance to 200 m.)
"Deep"		Remaining distance to bottom (or to 200 m.)

PHYSICAL CONDITIONS

Georges Bank (Fig. 1) is an elongated submarine plateau with a steep north-western face towards the Gulf of Maine and a gradual south-eastward tilt in the direction of the Continental Slope. The plateau is about 150 miles long and 100 miles wide. Depth of water varies from 200 m. at the edge of the bank to 5 m. on Georges Shoal in the northwest section. The depth of the major portion of the bank lies between 40 and 100 m.

Turbulence caused by tidal currents and winds results in vertical mixing of a large amount of the relatively shallow water overlying the bank. The mixing produces in this water mass a nearly uniform distribution of temperature and salinity from surface to bottom at all seasons of the year (Clarke, Pierce, & Bumpus 1943). That portion of Georges Bank over which nearly complete mixing is found has been called by these investigators the "Mixed Area"; all stations at which the salinity does not vary by more than 0.2 part per mille from surface to bottom are considered to lie within it and its position is shown on the distribution charts (Figs. 3-10) by a heavy broken line. The bank water of the Mixed Area thus contrasts sharply with the surrounding water masses which are typically stratified during all except the winter months.

Water temperatures in the Mixed Area vary less than 1.6° C. from surface to bottom and salinity changes less than 0.2‰. While these variations are not considered ecologically important as far as temperature tolerance is concerned a vertical gradient, even of 1.6° C., tends to create stability. Hence planktonic crustaceans cannot be carried by mixing from surface to bottom but have to pass through intermediate layers. Lateral mixing may occur in the intermediate layers. Turbulence expresses itself as lateral mixing in the presence of stability. Within the Mixed Area, wherever water is perfectly homogeneous, distribution of plankton is governed by vertical mixing or upwellings freely following tidal circulation and the disturbing effects which wind exercises on the surface. Since the larger Crustacea are caught both inside and outside of the Mixed Area and as they are believed to be species characteristic of mid-depth or bottom an examination of the effects of bottom temperatures on distribution will be discussed later in this paper.

In Table 1, bottom temperatures at stations within the 100 m. contour and at stations between the 100 m. and 200 m. contours are given for 1940 and 1941. The stations on the north edge of the bank between the 100 m. and 200 m. contours have been listed separately from those on the south edge of the bank in order to show differences that may exist between these two regions. The bottom temperatures of the north edge of the bank would be influenced by the mixing of bank water with generally cooler Gulf of Maine water, whereas the south edge of the bank would have bottom temperatures resulting from a mixing of bank water with warmer Atlantic slope water. For these reasons, the maximum and minimum values only for the bottom temperatures between 100 m. and 200 m. are given in Table 1. Average bottom temperatures for these deep stations would have little significance. Bottom temperatures at all stations inside the 200 m. contour for the six cruises are found in Figure 2. For stations off the bank the temperatures are for 200 meters.

Examination of Table 1 and Figure 2 shows that within the 100 m. contour average bottom temperatures may vary seasonally from 3° C. to 12° C.; within the 100 m. to 200 m. contours the same range of actual—not average—temperatures may be found

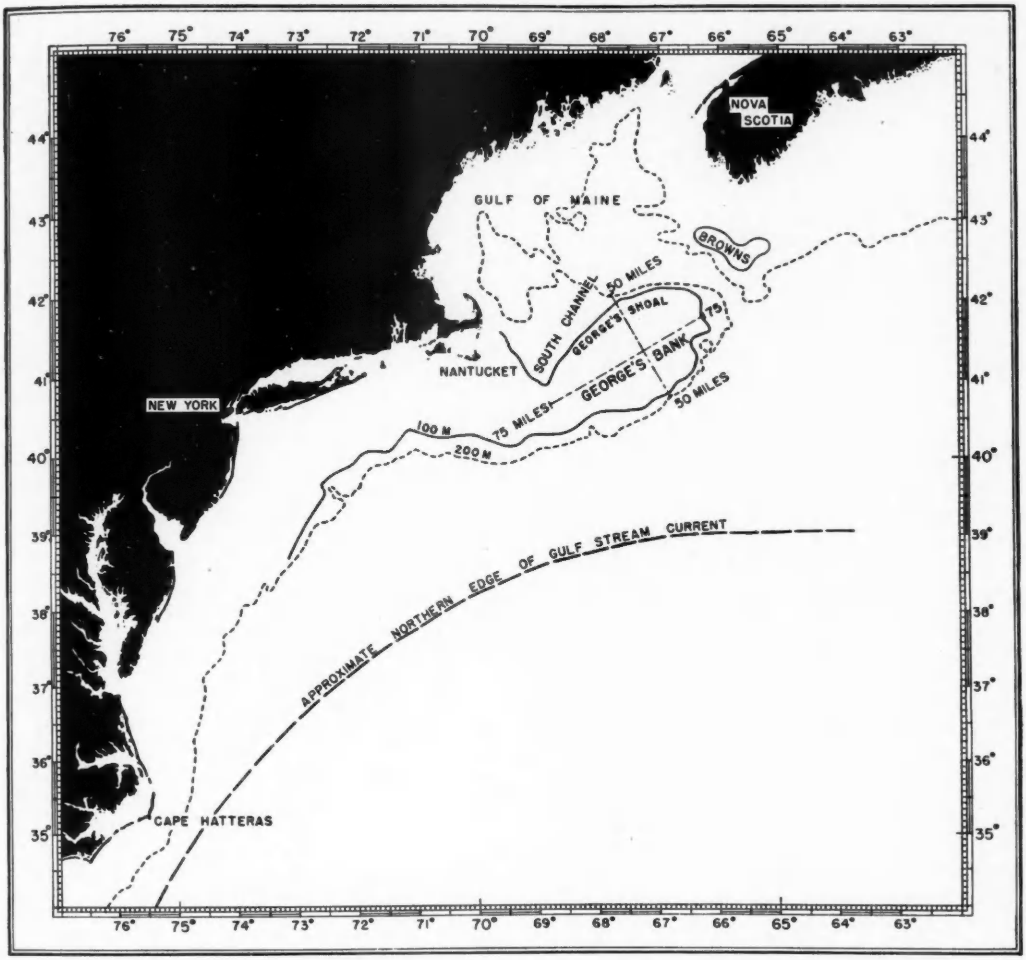

FIG. 1. Orientation map of Atlantic Coast. The location and size of Georges Bank are indicated.

when both the north and south edges of the bank are considered. Bottom water of the bank is warmest in September; within the 100 m. contour the average temperature is then warmer by approximately 3° C. than the maximum temperature of the deeper water. This condition is most probably the effect of solar heating and the transfer of warm surface water to the bottom by vertical mixing. Coolest bottom water temperatures are found in March and April. During winter Georges Bank water is colder than either Gulf or Maine or Atlantic slope water. Effect of winter cooling and summer heating is more pronounced in the well-mixed shoaler water. Warm slope water appears to have an influence on the bottom temperatures of the southern section of Georges Bank within the 100 m. to 200 m. contours since maximum temperatures of approximately 12° C. occur here as early as March. Cold water from the Gulf of Maine appears to influence bottom temperatures on the northern section of the bank because the highest temperature recorded here was approximately 6° C.

The water in the Mixed Area is believed to be relatively stationary, that is, there is little movement across it except perhaps during winter (Bigelow 1926). Around the northern, eastern, and southern margins of the bank, there is a well established clockwise current. Anomalous conditions occur from time to time along the edge of the bank probably influenced by this current. For example, during spring and summer on the southern seaward side of the bank, a tongue of cold water dovetails in between the warmer and fresh bank water on the north and the Gulf Stream on the south. This tongue, observed by Bigelow in 1924, and also during the present investigation, may serve to transfer Gulf of Maine water and its plankton on to Georges Bank (Clarke, Pierce, & Bumpus 1943).

Presumably fuana of the Mixed Area can reach

TABLE 1. Bottom temperatures at stations within the 100-meter contour and at stations between the 100-meter and 200-meter contours for 1940 and 1941. Stations on the north edge and south edge listed separately for purpose of comparison. Temperatures given in degrees centigrade.

DATE	Sept. 1939	Jan. 1940	Mar. 1940	April 1940	May 1940	June 1 1940	June11 1940	Mar. 1941	April 1941	May 1941	June 1 1941
CRUISE NO.	89	93	95	96	97	98	100	112	113	114	116
Maximum	16.2	6.0	3.9	4.3	5.8	8.2	10.2	3.9	4.9	6.0	8.0
Minimum	5.4	4.1	2.3	3.4	3.8	4.3	5.7	2.4	2.9	3.8	4.1
Average	11.5	4.7	2.8	3.6	4.7	6.2	7.4	3.0	3.9	4.9	6.2

BOTTOM TEMPERATURES AT STATIONS BETWEEN THE 100 M. AND 200 M. CONTOURS

NORTH EDGE OF BANK

DATE	Sept. 1939	Jan. 1940	Mar. 1940	April 1940	May 1940	June 1 1940	June 11 1940	Mar. 1941	April 1941	May 1941	June 1 1941
CRUISE NO.	89	93	95	96	97	98	100	112	113	114	116
Maximum	4.9	5.2	3.2	4.0	5.8	4.6	4.8	4.3	5.2	4.7	4.5
Minimum	4.6	5.1	2.6	3.0	3.0	2.9	3.0	3.6	4.0	4.4	4.4

SOUTH EDGE OF BANK

DATE	Sept. 1939	Jan. 1940	Mar. 1940	April 1940	May 1940	June 1 1940	June 11 1940	Mar. 1941	April 1941	May 1941	June 1 1941
CRUISE NO.	89	93	95	96	97	98	100	112	113	114	116
Maximum	9.4	6.0	11.5	11.2	8.1	10.3	10.8	11.7	5.2	8.6	7.7
Minimum	7.6	5.7	3.2	4.0	4.2	4.9	5.1	4.8	4.7	3.8	4.3

markedly different physical conditions only by migrating laterally out of it. Iselin (1939) has drawn attention to the possibility of lateral turbulence as a factor in the transport of plankton. When vertical stability is high, lateral turbulence is active (Parr 1936), hence the possibility of lateral transport of plankton on to Georges Bank from its margins or vice versa may be expected during early autumn, when conditions favoring stability usually prevail. But the intermingling of surrounding water with the Mixed Area is probably a slower process, and the degree to which the movements of crustacea during September within the Mixed Area is influenced by this transport is not yet clear. Study of the distribution of the larger Crustacea has on the whole not added to knowledge concerning the circulation over Georges Bank. Since these organisms can migrate vertically or even perhaps rest on the bottom for considerable periods they are inferior to more passive types as current indicators. Little is known about the nature of the bottom surface or the bottom fauna of Georges Bank. Dredging was carried on at 15 stations by Smith & Harger in 1874 and since then random bottom samples have been collected by the United States Coast and Geodetic Survey while making soundings on the bank. About thirty photographs of the bottom were made by automatic underwater cameras during the present investigation by members of the Oceanographic Institution (Ewing, Vine, & Worzel 1946; Ewing, Wollard, Vine & Worzel 1946).

Sand, either fine or coarse, appears according to these sources to cover the major portion of Georges Bank; occasionally it is mixed with broken shells, mud, or pebbles. Stony bottom also occurs. Ripple marks on the mud or sand, indicating the effect of bottom currents, appear in the photographs and such invertebrates as sand dollars, hermit crabs, star fish, and sea clams are also seen in many of the pictures.

Types of invertebrates taken by the dredge on Georges Bank (Smith & Harger 1874) were: Crustacea; Annelida; Mollusca; Echinodermata. There were approximately 30 to 40 species of each. Several of the crustacean species taken by the dredge were also caught by the stramin net in the present investigation. The decapod, *Dichelopandulus leptocerus*, was taken many times in the dredge by Smith & Harger and was reported as "common"; in the stramin net it was caught occasionally and had a relative numerical abundance of 0.3% per standard haul for all cruises. Of the amphipods caught by the dredge, there were twelve species also found in the stramin collection. Only two of these, *Pontogenia inermis* and *Unciola irrorata*, were taken at more than 50 out of a total of 296 stramin hauls, however; and of these two, only *Pontogenia inermis* occurred many times, having a relative numerical abundance of 1.5% per standard haul for all stations. The most abun-

dant Crustacea taken by the stramin net, such as *Themisto compressa, Monoculodes edwardsi, Neomysis americana, Thysanoessa inermis*, or *Crago septemspinosus*, were not taken in the dredge by the 1874 expedition.

VOLUMETRIC ABUNDANCE OF THE PLANKTON

The volumetric abundance of all the plankton taken in the stramin net was estimated on the basis of amount caught per standard haul for each station. The average volume per standard haul for each cruise was then calculated. These data were divided into average volumes for day hauls (6 a.m. to 6 p.m.) and night hauls in order to determine whether any differences in volume occurred due to various diurnal changes in the activity of the plankton which might affect the catches.

TABLE 2. Comparison of total plankton volumes caught by stramin net. Average volumes per standard haul for total plankton at all stations in each cruise and comparison of average volumes for day and night hauls.

CRUISE	Date	AVERAGE VOLUME IN CC.		
		Total	Day	Night
89....	September 1939	53	51	62
93....	January 1940	66	51	75
95....	March 1940	35	43	26
96....	April 1940	75	82	66
97....	May 1940	132	86	184
98....	June 1, 1940	188	166	216
100....	June 11, 1940	141	160	126
112....	March 1941	63	36	83
113....	April 1941	42	44	39
114....	May 1941	54	46	64
116....	June 1, 1941	214	251	190

An examination of Table 2 shows that for the plankton as a whole individuals are caught by the stramin net with approximate equal efficiency during both night and day. In only two cruises was either the night haul greater than the day haul, or vice versa, by more than two fold. For May, 1940, there were four unusually large night tows that consisted chiefly of sagittae. If these values, which range from 246 cc. to 634 cc., are omitted from the calculations, the average of 113 cc. results, which is less than twice the day haul of 86 cc. For March, 1941, if two unusually large night hauls of 438 cc. and 250 cc. due to an abundance of *Neomysis americana* are omitted, the average night value is reduced to 50 cc., which is less than twice the average day value of 36 cc. Thus the plankton as a whole does not show a marked tendency to escape the net by seeing and avoiding it any more easily during day than at night.

The vertical movements of some individual species in the plankton will be discussed in a subsequent section of this paper, but an examination of Tables 3 and 4 show that for the plankton as a whole there is no marked vertical migration during day or night. This condition, although contrary to what might be expected, probably indicates that while individual species may migrate vertically, the extent of their migration is either relatively small or that the movements of the various species cancel each other. Turbulence may also tend to confuse the pattern of diurnal movement. Data from April and June, 1940 were used in the tables because of the number of night and day hauls and the variety of organisms in the plankton sampler catches during those cruises.

The question may be raised that the plankton sampler or stramin net failed to catch organisms that remained very close to or rested on the bottom during the day. Examination of the plankton sampler catches, in addition to those given in Tables 3 and 4, showed that amphipods were more consistently caught at Second-depth or Deep levels by day than were euphausiids. Hence, it is unlikely that unsampled schools of euphausiids were present, for although the active euphausiids might be supposed to avoid easily the small mouth of the plankton sampler, good agreement with stramin net catches was obtained on many occasions when euphausiids were present. Clarke, Pierce, & Bumpus (1943) also demonstrated that the catch of the plankton sampler for active animals can be relied upon.

Table 2 illustrates the gradually increasing and decreasing monthly variations in the average volumes of plankton that corresponded to each cruise. In 1940, minimum and maximum average values of 35 cc. and 188 cc. per standard haul were found in March and June 1 respectively; or, assuming that an average of 300 $m.^3$ of water was filtered during the

TABLE 3. Comparison of the vertical distribution of the more numerous species in plankton sampler hauls. The average number per cubic meter when present and the average percentage of the total number of organisms taken at each level at stations in Cruise 96, April, 1940, for day and night hauls is presented. Species which occurred at one station only in the day and night hauls are omitted. The number of stations at which each species was caught is given in parenthesis in the first two columns.

Organisms	No. OF STATIONS		AVERAGE No. /m³ WHEN PRESENT		AVERAGE PERCENTAGE AT EACH LEVEL		
	Day	Night	Day	Night		Day %	Night %
STATIONS AT WHICH THE SECOND DEPTH HAUL EXTENDED TO THE BOTTOM.							
Monoculodes edwardsi......	6(4)	9(9)	1.2	0.9	Shallow	0	23
					2nd Depth	100	77
Neomysis americana.....	6(1)	9(2)	0.6	0.2	Shallow	0	61
					2nd Depth	100	39
Thysanoessa inermis.......	6(1)	9(4)	0.2	0.7	Shallow	100	66
					2nd Depth	0	
STATIONS AT WHICH THE SECOND DEPTH HAUL DID NOT EXTEND TO THE BOTTOM.							
Themisto compressa.....	7(3)	3(1)	0.3	0.4	Shallow	52	100
					2nd Depth	48	0
					Deep	0	0
Monoculodes edwardsi......	7(2)	3(1)	1.2	0.9	Shallow	48	0
					2nd Depth	0	78
					Deep	52	22
Thysanoessa inermis.......	7(4)	3(2)	0.1	0.2	Shallow	0	40
					2nd Depth	13	60
					Deep	87	0

TABLE 4. Comparison of the vertical distribution of the more numerous species in plankton sampler hauls. The average number per cubic meter when present and taken at each level at stations in Cruise 100. June 11, 1940, for day and night hauls is presented. Species which occurred at one station only in the day and night hauls are omitted. The number of stations at which each species was caught is given in parenthesis in the first two columns.

Organisms	No. of Stations		Average No. /m³ When Present		Average Percentage At Each Level		
	Day	Night	Day	Night		Day %	Night %
STATIONS AT WHICH THE SECOND DEPTH HAUL EXTENDED TO THE BOTTOM.							
Monoculodes edwardsi	12(3)	4(4)	5.0	0.5	Shallow	0	8
					2nd Depth	0	92
Neomysis americana	12(4)	4(1)	43.3	0.2	Shallow	48	10
					2nd Depth	52	100
STATIONS AT WHICH THE SECOND DEPTH HAUL DID NOT EXTEND TO THE BOTTOM.							
Themisto compressa	10(6)	10(3)	0.2	0.1	Shallow	40	80
					2nd Depth	21	13
					Deep	39	7
Monoculodes edwardsi	10(0)	10(6)	0	0.5	Shallow	0	16
					2nd Depth	0	33
					Deep	0	51
Megancytiphanes norvegica	10(0)	10(3)	0	0.3	Shallow	0	50
					2nd Depth	0	48
					Deep	0	2
Thysanoessa inermis	10(6)	10(2)	1.0	0.8	Shallow	0	0
					2nd Depth	18	50
					Deep	82	50

standard haul (for discussion of standard haul, see page 235) the range is from a March minimum of 0.1 cc./m.³ to a June maximum of 0.6 cc./m.³ The same general rise also occurred in 1941 except that in this year the low point came in April, a month later than in 1940. In both years, there was approximately a five-fold difference between the greatest and least average monthly volumes.

The maximum individual catches were also considered. If all volumes of more than 300 cc. per standard haul or approximately 1 cc./m.³ were selected from the data, no cases were found for September, 1939, nor for January and March, 1940. One case occurs in April, three in May and five each June 1 and June 11. Of these, the highest value does not exceed 1200 cc. per standard haul, or approximately 4 cc./m.³ During 1941, there was one case in March, none in April or May and nine cases in the June 1 Cruise. The 1941 results closely resembled those found in the preceding year. It is important to note that the maximum average volumes and the maximum individual volumes both occurred in June.

An estimate of the plankton production on Georges Bank can also be judged from a comparison made between stramin net average volumes and the average volumes taken by the plankton samplers at the same station. The plankton sampler data was obtained from another part of the Georges Bank investigation.

The stramin net had a #00 silk inner tail and thus caught some of the smaller organisms; the fine meshed #2 silk nets of the plankton sampler caught both large and small organisms. Thus, the catches to some extent include the same fauna. From Table 5, it is seen that the volumes of the plankton sampler are usually greater than those of the stramin net volumes, the variation being less during the January-March period when there were presumably smaller numbers of the smallest plankton available, and largest during the June period when maximum numbers of the smallest plankton might occur. This, no doubt, is because that bulk of the smaller organisms which the stramin net fails to catch, is greater in volume than that bulk of the larger plankton caught by the stramin net. With these reservations in mind, examination of Table 5 indicates the approximate richness of the plankton on Georges Bank. Sampler average volumes range from 0.2 cc./m.³ to 1.7 cc./m.³; stramin average volumes from 0.2 cc./m.³ to 0.7 cc./m.³

TABLE 5. Comparing the average volumes from plankton sampler and stramin net. Average volumes calculated in cubic centimeters per cubic meter taken by plankton sampler and stramin net when both were towed at the same station.

Cruise	Plankton Sampler cc. /m³	Stramin Net cc. /m³
93 January 1940	0.22	0.22
95 March 1940	0.48	0.11
96 April 1940	0.99	0.25
97 May 1940	1.13	0.44
98 June 1, 1940	1.21	0.62
100 June 11, 1940	1.23	0.47
112 March 1941	0.22	0.21
113 April 1941	1.16	0.14
114 May 1941	1.16	0.18
116 June 1, 1941	1.78	0.71

Again realizing that the stramin net fails to retain some of the smaller organisms, a rough comparison (Table 6) can also be made with data given by Bigelow & Sears (1939) which summarizes the more extensive measurements of plankton volumes along the east coast of North America and North European waters.

Bigelow & Sears regard the most representative maximum single hauls of plankton yet recorded from American waters to be: 6.9 cc./m.³ taken in the offing of New Jersey; 2.0 cc./m.³ taken in the Gulf of St.

TABLE 6. Volumes of plankton along the east coast of North America, Northern Europe and Georges Bank.

Locality	Estimated cc./m³
Cape Cod to Chesapeake Bay	0.4 - 0.8
Gulf of Maine	0.05 - 0.7
Nova Scotia Shelf	0.3 - 0.4
Iceland to Ireland	0.2 - 0.8
Norwegian Sea to North Sea	0.3 - 0.6
Present investigation of Georges Bank:	
Stramin Net	0.2 - 0.7
Plankton Sampler	0.2 - 1.7

Lawrence; and 1.0 cc./m.^{3} from the Scotia Shelf and from West Greenland. In the light of these statements it is reasonable to conclude that Georges Bank supports a rich plankton.

SPECIES COMPOSITION OF THE PLANKTON

In the collection of Plankton made by the 1.5 meter stramin net, a total of 57 species of larger Crustacea were identified. These species are listed below.

DECAPODA
Crago septemspinosus (Say)
Dichelopandulus leptocerus (Smith)
Spirontocaris liljeborgii (Danielssen)

MYSIDACEA
Erythrops erythrophthalma Goës
Neomysis americana (Smith)

EUPHAUSIACEA
Euphausia krohnii Brandt
Meganyctiphanes norvegica (M. Sars)
Nematoscelis megalops G. O. Sars
Thysanoessa inermis (Krøyer)

AMPHIPODA
Annonyx nugax (Phipps)
Acanthonotosoma serratum (O. Fabricius)
Autonoe websteri (G. O. Sars)
Apherusa tridentata (Bruzelius)
Ampelisca spinipes Boeck
Ampelisca macrocephala Lilljeborg
Argissa typica Boeck
Byblis gaimardii (Krøyer)
Bathyporeia norvegica G. O. Sars
Calliopius laeviusculus (Krøyer)
Ericthonius brasilensis (Dana)
Eusirus cuspidatus (Krøyer)
Rhachotropis inflata G. O. Sars
Stegocephalus inflatus Krøyer
Syrrhoe crenulata Goës
Tiron acanthurus Lilljeborg
Tmetonyx noblis (Stimpson)
Eusirus propinquus G. O. Sars
Hoplonyx cicada (O. Fabricius)
Hyperia galba (Montagu)
Haliragès fulvocintus (M. Sars)
Hyperoche kroeyeri Bovallius
Haloops tubicola Lilljeborg
Hippomedon serratus (Holmes)
Hippomedon propinquus G. O. Sars
Hippomedon denticulatus (Bate)
Leptocheirus pilosus Zaddach
Menigratus obtusifrons (Boeck)
Melphidippa goesi Stebbing
Melphidippa spinosa (Goës)
Melita dentata (Krøyer)
Monoculodes edwardsi Holmes
Paradaliscidae sp.
Probomedeia fasciata Krøyer
Pontoporeiidae sp.
Photis reinhardi Krøyer
Pleustes panoplus (Krøyer)
Parathemisto obliva (Krøyer)
Pontogenia inermis (Krøyer)
Phoxocephalus holboli (Krøyer)
Rhachotropis oculata (Hansen)
Tmetonyx quadratus Kunkel
Themisto compressa Goës f. *compressa* Goës
Thyposa minuta Boeck
Unicola irrorata Say
Vibilia armata Bovall

SELECTION OF PREDOMINATING SPECIES

The ecological importance of the larger Crustacea can be judged in two ways: by frequency of occurrence—being caught at many stations over a wide area; or by relative abundance at any station. An organism that swarmed in great numbers at few stations might be just as important as one which occurred sparsely at many. To simplify selection of predominating species among these larger Crustacea, it was decided to choose arbitrarily the criteria of 50 hauls in order to establish a frequency of occurrence (Table 7). On this basis of the ten frequently occurring Crustacea, Monoculodes and Thysanoessa, were caught in more than 50% of all hauls.

TABLE 7. Frequency of occurrence of the crustacean species. Species of Crustacea which occurred in more than 50 out of total of 332 stramin net hauls and the number of hauls in which they occurred.

SPECIES	No. of Hauls
Monoculodes edwardsi	182
Thysanoessa inermis	171
Decapod larvae	133
Themisto compressa	101
Crago septemspinosus	98
Schizopoda immature[1]	91
Neomysis americana	89
Meganyctiphanes norvegica	72
Dichelopandulus leptocerus	67
Pontogenia inermis	64

[1] The immature mysids and euphausiid larvae were grouped together as Schizopoda immature.

If the relative abundance of the crustacea is now considered, as in Table 8, in which the species more abundant than 200 and 500 per standard haul are shown, nine of the most frequently occurring (Table 7) again appear. The species are marked by an asterisk in Table 8. These Crustacea are therefore both widely distributed over Georges Bank and also occur in significant numbers.

TABLE 8. Abundance of the crustacean species. Cases in which each species were more abundant than the indicated numbers.

	NUMBER OF STANDARD HAULS.	
SPECIES	*More than 200 Specimens*	*More than 500 Specimens*
**Monoculodes edwardsi*	55	17
*Schizopoda immature	36	18
*Decapod larvae	35	12
**Neomysis americana*	23	15
**Crago septemspinosus*	7	1
Euphausia krohnii	6	1
**Themisto compressa*	5	0
**Thysanoessa inermis*	4	2
**Meganyctiphanes norvegica*	4	1
**Pontogenia inermis*	3	2
Nematoscelis megalops	3	0
Erythrops erythropthalma	1	0

Seasonal changes in the catches of the larger Crustacea is set forth in Table 9, which presents for each cruise the average number per stramin haul of the more abundant types and plainly illustrates both the relative plentifulness and widespread distribution of such species as Monoculodes, Thysanoessa, Neomysis, and Crago.

TABLE 9. Average number per standard haul per cruise of the species most abundant in Table 7. Numerals in parentheses represent the number of hauls at which organisms were caught during each cruise.

CRUISE NO.	89	93	95	96	97	98	100	112	113	114	116
DATE	Sept. 1939	Jan. 1940	Mar. 1940	Apr. 1940	May 1940	Jun. 1, 1940	Jun. 11, 1940	Mar. 1941	Apr. 1941	May 1941	Jun. 1, 1941
Total hauls made	36	13	28	26	30	36	36	33	34	28	32
Species											
Monoculodes edwardsi	120(15)	319(11)	45(14)	254(22)	218(22)	41(19)	79(12)	63(16	64(14	32(20)	59(21)
Pontogenia inermis	9(7)	85(4)	0.6(4)	5(9)	0.4(4)	1(5)	3(2)	1(6)	2(9)	33(8)	1(6)
Themisto compressa	71(31)	87(12)	0.3(2)	0(0)	1(7)	1(10)	1(8)	0.5(7)	.07(3)	2(10)	7(10)
Neomysis americana	75(5)	250(6)	0.3(4)	306(10)	39(10)	1(2)	1(3)	581(14)	125(12)	251(13)	31(9)
Thysanoessa inermis	47(15)	26(8)	13(20)	14(21)	13(20)	0.2(3)	1(5)	62(29)	8(15)	12(25)	1(7)
Meganyctiphanes norvegica	89(23)	1(2)	4(7)	6(6)	4(4)	3(4)	7(4)	6(7)	9(4)	16(5)	9(6)
Euphausia krohnii	91(11)	28(4)	0.5(2)	5(2)	4(2)	3(2)	7(3)	0(0)	.07(1)	0.2(1)	11(3)
Schizopoda immature	0(0)	2(2)	0(0)	1(1)	19(2)	134(20)	169(32)	1(1)	0(0)	14(7)	998(29)
Decapod larvae	141(23)	1(1)	123(2)	10(3)	73(10)	85(15)	63(24)	7(5)	59(18)	115(23)	684(5)
Crago septemspinosus	59(9)	71(6)	1(7)	11(15)	30(13)	2(6)	1(7)	14(13)	5(7)	3(8)	8(7)

Certain species have been mentioned as occurring frequently but only in small numbers, others have reversed this trend. If the organism with a low relative abundance is a large crustacean, and thus important in the food cycle, this fact must be weighed when the ecological importance of the species is considered. For instance, Dichelopandulus, found among the ten most frequently occurring species has a fairly wide distribution on the bank, but the largest single catch of it was 172 per standard haul. Usually it occurred in small numbers and averaged one per standard haul per cruise. Presumably this species keeps rather close to the bottom and only small numbers normally come within range of the net or the prawns may escape capture by actively swimming. Because of its size and its wide distribution, however, we include Dichelopandulus among the ten predominating species in the collection.

The three organisms listed in Table 8 but not found among the most frequently occurring species; namely, Euphausia, Nematoscelis, and Erythrops which occurred in 31, 47, and 34 hauls respectively, are examples of organisms which do not have a widespread distribution on Georges Bank but are occasionally caught in moderately large numbers there. Erythrops is almost invariably taken on the south edge of the bank between the 100 m. and 200 m. contours. Nematoscelis and Euphausia are usually found beyond the 200 m. contour on the slopes of the bank, not always, however at the same station. Since these organisms are more typically slope than bank types, they were not numbered in the list of predominating species.

To conclude, therefore, it can be said that with exception of Dichelopandulus, the ten most frequently occurring species are also found in greatest relative abundance on the bank. Such species as Euphausia, Nematoscelis, and Erythrops, which sometimes are caught in abundance, were not taken more frequently because they were not typically bank inhabitants and were only caught when stations were made at the edge of the bank near the 200 m. contour. Only a few such stations were made on each cruise. There was no other species which occurred in numbers more limited than 200 per standard haul, or in less than 50 hauls the size of which might make it especially important in the food cycle of Georges Bank. Therefore, the evidence presented by the preceding data suggests that the following crustaceans are the predominating species in the stramin net collection.

Monoculodes edwardsi
Themisto compressa
Pontogenia inermis
Neomysis americana
Thysanoessa inermis
Meganyctiphanes norvegica
Crago septemspinosus
Dichelopandulus leptocerus
Schizopoda immature
Decapod larvae

The distribution of these species on Georges Bank will be discussed in the following section.

CONSIDERATION OF PREDOMINANT SPECIES

MONOCULODES EDWARDSI

OCCURRENCES

Monoculodes edwardsi comprises an average of 40% of the amphipods taken at all stations, and thus is pre-eminently the most abundant species of this

group. It is odd that this amphipod, apparently so numerous on Georges Bank, had never previously been reported from this region. Individuals had been taken in New England waters for it was first described as a new species from Woods Hole by S. J. Holmes in 1903. Shoemaker (1930) reports that 500 specimens were taken by dredge and young fish trawl at eight stations in the Gulf of St. Lawrence and the Magdalen Islands at depths varying from 10 m. to 75 m., the deepest at which it had previously been reported. In the present collection, specimens were caught at depths from 40 m. to 120 m. This amphipod has not yet been noted outside the northeast coast of North America. Dr. Shoemaker kindly examined some of the amphipods of the present collection and confirmed the identity of *Monoculodes edwardsi*.

The eleven cruises to Georges Bank made by the *Atlantis* obviously extended over a comparatively short period. Additional data over a longer span of years concerning the occurrence of Monoculodes might reveal that it periodically fluctuated in abundance on the bank, which would perhaps account for the failure of previous expeditions to capture this now abundant amphipod.

Inspection of the distribution chart Figure 3, shows that Monoculodes may have a widespread disposition inside the 100 m. contour of Georges Bank throughout most of the year. During eleven cruises, it was taken in deeper water only in the following cases: beyond the 100 m. line, ten hauls chiefly with catches less than ten per standard haul; beyond the 200 m. line, three hauls with all catches less than five per standard haul. The amphipod was taken on or beyond the 100 m. line more frequently on the north edge of the bank than on the south edge.

The distribution pattern for Monoculodes was the same in both 1940 and 1941, but the average catches (Table 9) were smaller in the latter year, being 54 per standard haul per station per year.

Although Monoculodes may be found over most of the bank throughout the year, it is completely absent from a large portion of the shallow central bank during June, as a scrutiny of the charts for June 1940 and 1941 (Fig. 3) will show. With the approach of summer, the amphipod appears to be restricted to a relatively narrow belt along the 100 m. contour of the south edge of the bank. Presumably, its occurrence is favored by cooler water now found between the warmest bank water covering the central regions and the warm Atlantic water of the south slope. Prevailing bottom temperatures (Fig. 2) might suggest this view. Wide differences in numbers per standard haul between stations practically adjacent characterize the distribution of Monoculodes during spring and early summer. These differences, easily seen for June 1940 and June 1941 in Figure 3, might indicate that the organism is here actively avoiding unfavorable environmental conditions. However, a distribution based on low temperatures fails to explain the widespread occurrence of Monoculodes in September when the bank water is relatively warm (Fig. 2). It is possible, as Edwards & Irving (1943) have shown for certain Crustacea, that this amphipod has the ability to become adjusted to seasonal changes in temperature, and during spring, avoids water to which it later becomes adjusted.

To account for distribution of the species solely on the basis of variations in water temperatures oversimplifies the question, however, and neglects such factors as: influence of water movement, centers of reproduction, accessibility of food, or the nature of the bottom. The possible effect of some of these factors can, unfortunately, only be surmised in the absence of direct evidence. Inspection of Figure 3 shows that the homogeneous water of the Mixed Area, indicated by a heavy broken line on each chart, does not limit the distribution of Monoculodes. Substantial catches are commonly made both inside and outside the Mixed Area. Occurrence of Monoculodes is thus less closely circumscribed by water of the Mixed Area than was the pelagic chaetognath *Sagitta elegans* investigated by Clarke, Pierce, & Bumpus (1943). This widespread horizontal distribution of Monoculodes, coupled with the length of time it flourishes on the bank during the year, suggests that reduction in numbers and decrease in distribution during spring may as probably be related to death of adults after breeding as to a reaction to unfavorable ecological factors in the environment, since the organism appears to be indigenous to Georges Bank and not a temporary resident.

Largest single catches of Monoculodes were made in January, April, May, June and September in 1940 and during April and June in 1941. Thus, there does not seem to be a marked seasonal maximum. The peak catches were made at stations where the bottom temperatures varied from 11° C. to 3° C. If the catches of more than 500 per standard haul are considered the data can be arranged as in Table 10.

TABLE 10. Cruises having catches of more than 500 per standard haul.

Cruise		No. of Hauls	Bottom T°
89 Sept.	1939	2	11° C.
93 Jan.	1940	4	5° C.
95 March	1940	–	
96 April	1940	3	3° C.
97 May	1940	4	5° C.
98 June	1, 1940	–	
100 June	11, 1940	2	6° C.
112 March	1941	–	
113 April	1941	1	4° C.
114 May	1941	–	
116 June	1941	1	5° C.

Of the 17 catches having more than 500 per standard haul, 15 were made in the southwest or south central region of the bank between the 50 m. and 100 m. contours; hence this area may be considered the region of maximum abundance. Concentrations usually dwindle rapidly beyond the 100 m. line at the margin of the bank.

Vertical distribution of Monoculodes (Tables 3 and 4), indicates that in general there were fewer organisms in the shallow stratum than in the second

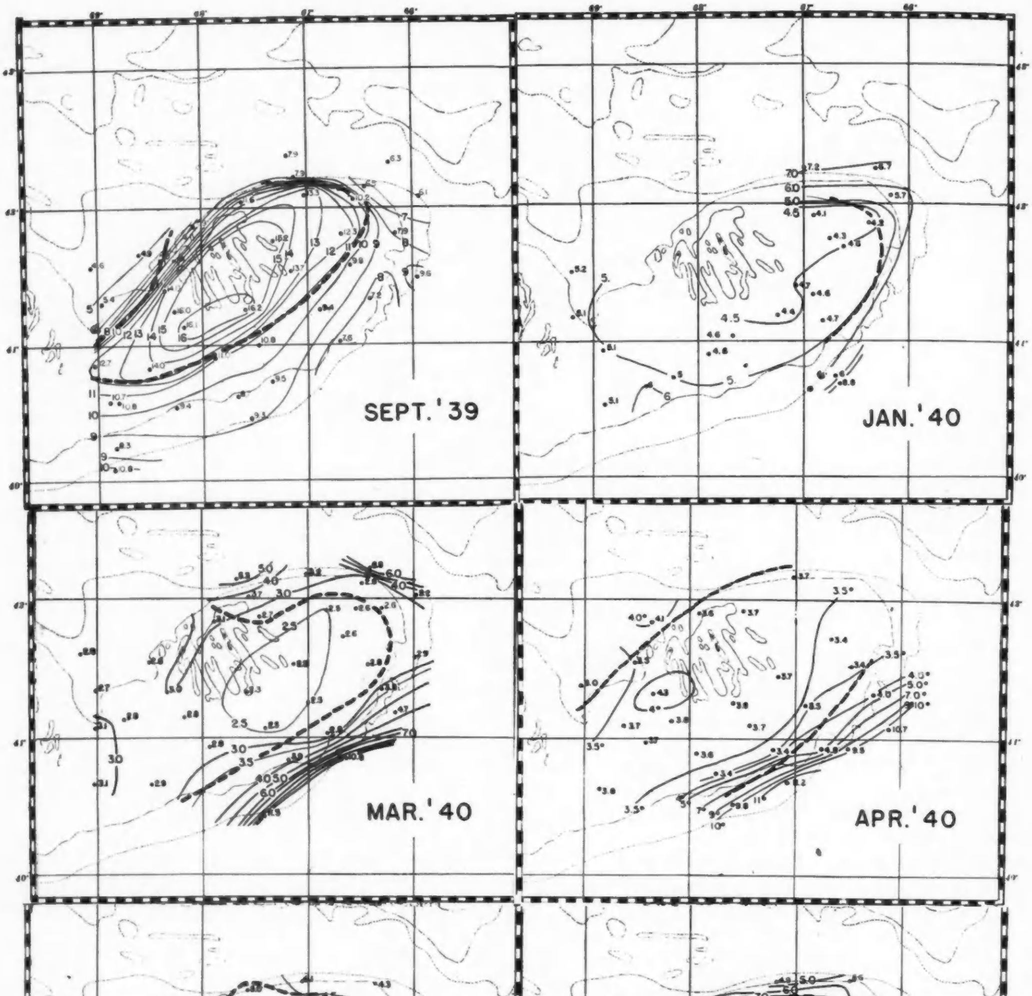

FIG. 2. Temperatures in degrees centigrade at the bottom of Georges Bank during September 1939, January, March, April, May and June 1940. Boundary of Mixed Area shown by heavy broken line.

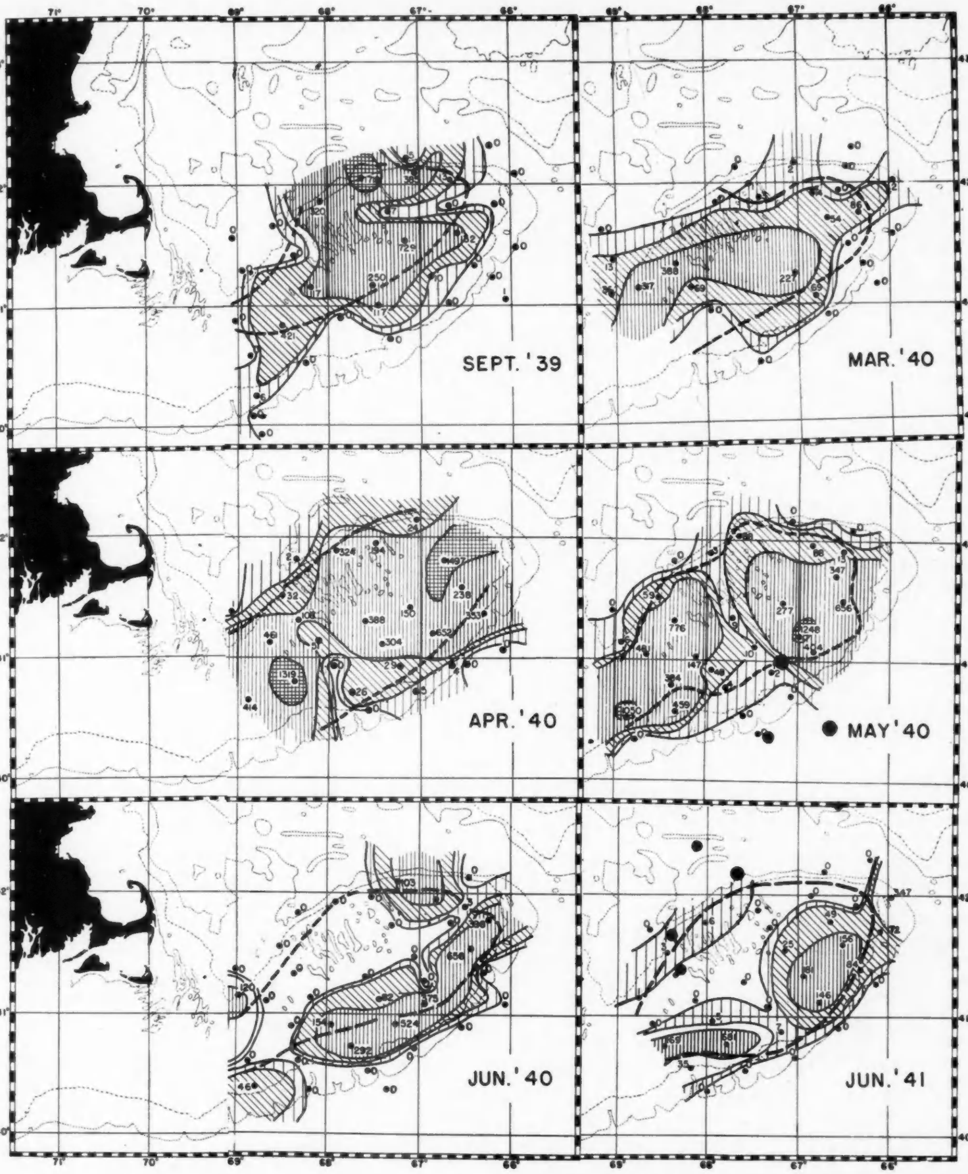

FIG. 3. Distribution of *Monoculodes edwardsi* on Georges Bank for September 1939, March, April, May and June 1940, and June 1941. Station positions designated by black dots. Numbers indicate individuals per standard haul of stramin net. Boundary of Mixed Area shown by heavy broken line. Contour lines representing concentrations of 1, 10, 100, 1000, have been drawn on all distribution charts. Progressively dense cross-hatching indicates areas of increasing numerical abundance.

depth of deep stratum. There was some tendency to move upward at night, but even at night there were more individuals caught at the deeper levels. In other cruises, not given in the tables, Monoculodes was rare in the shallow stratum.

BREEDING AND GROWTH

Comparatively little is known about the life history of amphipods. Holmes (1901) states, "aquatic amphipods are negatively phototropic,—fertilization takes place immediately after the female moults." Smallwood (1905) could determine no age groups for *Orchestra palustris*, a terrestrial amphipod, owing to wide variations in length. Eggs required 12 days to hatch in July. Skutch (1926) studied the tube build-

ing amphipod of Maine tidal pools, *Amphito rubricata*, and reports that breeding occurred from July until late August, egg bearing females, and females with young were taken throughout this period. Dunbar (1945) states that *Themisto libellula*, important as the chief food for harbour seals in the coastal waters of Baffin Land, is positively phototrophic, can grow as much as 2 mm. per month, has a breeding period during spring and probably a second in autumn so that two generations exist simultaneously.

Concerning the habits of planktonic amphipods in the open ocean, even less is known. On Georges Bank in the northeast section during September, 12 Monoclodes, 3-4 mm. in length were caught. In January, 16 specimens 3-7 mm. in length were caught, on the southwest section. Large numbers of adults were caught in these areas at the same time. During May and June, both the Plankton sampler and stramin net caught many female Monoculodes carrying eggs in brood pouch. With the exception of the young stages caught in September and January, no marked variation in size was noticeable among Monoculodes population. Individuals were measured from time to time to check their lengths against the adult size of 9 mm. given by Shoemaker. Very little variation from this length was found in the collections.

The occurrence of egg-bearing females in June and young stages in September and January indicate that the reproduction period on Georges Bank probably takes place during summer. Adult Monoculodes can be caught throughout the year on Georges Bank.

Fish (1925) examined the plankton of the Woods Hole region by daily tows throughout the year and recorded the appearance and disappearance of individual members of the fauna. Fish states that "*Monoculodes edwardsi* breeds from November to January." This conclusion was reached because Monoculodes, which he considered benthonic, appeared in the plankton tows at that time and not because egg-bearing females or larvae were found in the tows. On Georges Bank Monoculodes was not completely benthonic, it was sometimes pelagic and the bank breeding period previously mentioned as probably lasting through summer covers a different interval than the breeding period at Woods Hole. The appearance of Monoculodes at Woods Hole in November, however, may have been related to the sudden change in the temperature of the well-stirred Woods Hole waters which averaged, as data in Fish's report show, 20° C. from June to September. During October the temperature began to fall and in November dropped suddenly from about 13° C. to 4° C. When Monoculodes was appearing in the plankton at Woods Hole, from November until it disappeared in January, the temperatures ranged from 10° C. to 0° C. Distribution of this amphipod on Georges Bank shows that while the crustacean was sometimes caught in areas having bottom temperatures as high as 16° C., it was usually found in colder water. Hence one may speculate that the occurrence of Monoculodes in the Woods Hole plankton is associated with the November temperature change and therefore may not be solely due to a breeding migration.

THEMISTO COMPRESSA

OCCURRENCES

Two representatives of *Themisto*, the forms *compressa* and *bispinosa*, have long been known to abound off the northeast coast of the United States, typically on the coastal banks. These two "formae" are, however, now considered as one species (Stephensen 1924) and in this paper they are treated as *Themisto compressa*.

Bigelow (1926) states "Themisto is one of the most characteristic, if not abundant, members of the plankton of the offshore waters of the Gulf of Maine where it was taken at approximately 90 per cent of the stations outside the 100 meter contour during July and August."

In the present investigation (Fig. 4) Themisto was widely dispersed over Georges Bank in September. At 10 stations there were catches of more than 100 per standard haul. In January fewer stations were made and the entire bank was not sampled but catches during January suggest that no marked change in distribution had occurred since September. Average number of individuals caught per standard haul in January was somewhat less than during the fall cruise, although in the southwest area there were three rich tows, one being 426 per standard haul, which exceeded the highest individual catch of September. Distribution in both 1940 and 1941 was very similar; the May and June 1941 catches were slightly larger than in the previous year.

From March to May, Themisto is practically absent from the major portion of the bank. Individuals begin to reoccur during May and June along the north and south margins (Fig. 4). Hauls of Themisto were made both inside and outside the Mixed Area. Catches outside the Mixed Area are usually larger even in September when the organism is widely distributed over the bank.

These facts suggest that Themisto always present in the Gulf and offshore (Bigelow & Sears 1939) is borne to the bank either by water movement or by the animal's own power of locomotion. If water movement alone was involved Themisto would probably not be so conspicuously absent from the bank during winter and spring. At least some of the animals swept on and off the bank would be caught. Therefore, it would seem that in spite of water movement the organism is able by its own efforts to avoid being carried to the bank. The reason for its nonoccurrence during winter may thus indicate lack of favorable environmental condition for growth or breeding.

One may judge from the distribution of Themisto during September and January that maximum occurrence of the organism is associated with comparatively high temperatures (6° C. to 14° C.) on Georges Bank. Average number per standard haul per cruise indicated a fall maximum and a midwinter minimum (Table 8). Bigelow (1926) found a somewhat similar incidence in the Gulf of Maine.

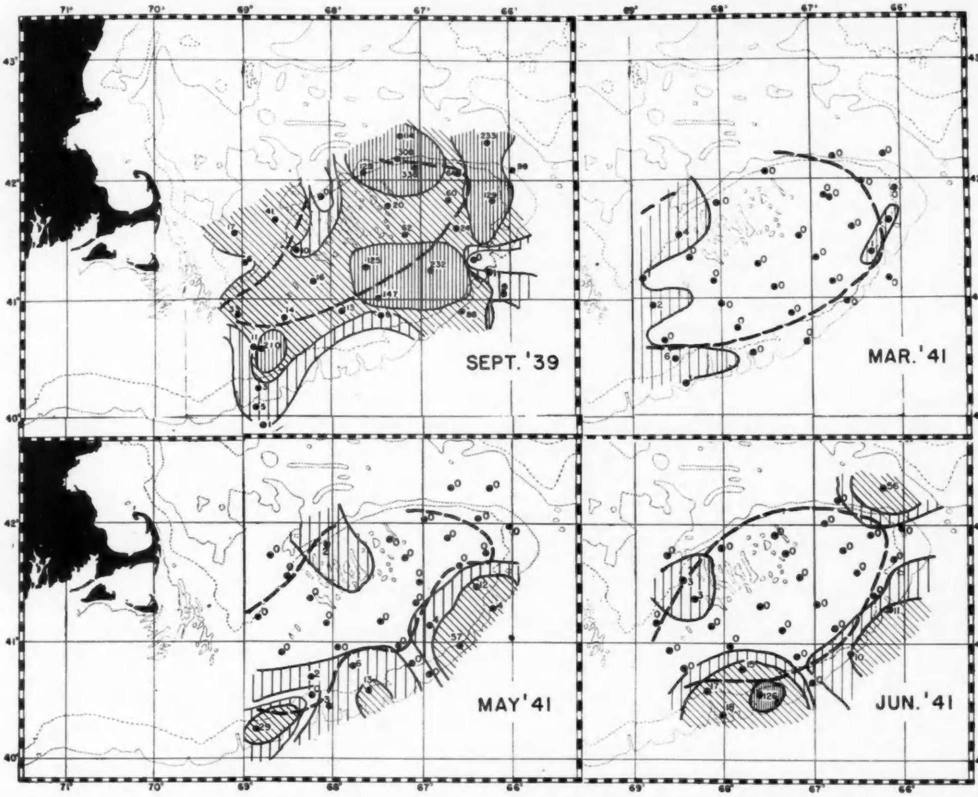

FIG. 4. Distribution of *Themisto compressa* on Georges Bank for September 1939, March, May, and June 1941. Station positions designated by black dots. Numbers indicate individuals per standard haul of stramin net. Boundary of Mixed Area shown by heavy broken line.

A summer and early autumn maximum contrasted with an early spring minimum. Bigelow also states that Themisto, while abundant in the Gulf, is rarely caught off Nova Scotia. The cold waters of that area may form an unfavorable environment for it.

Distribution of Themisto on Georges Bank suggests, therefore, that both water movement and suitable environmental conditions, of which temperature is an important factor, are associated with its maximum occurrence. Extremes of temperature, above 15° C. and below 5° C., are apparently unfavorable for it. The animal's minimum occurrence is apparently due to its ability to avoid these conditions.

The vertical distribution of Themisto (Tables 3, 4) indicates that rarely was it caught on shoal areas of the bank where the second-depth stratum extends to bottom. Wherever deeper hauls were made, however, largest catches occurred principally in the shallow stratum and next in the second-depth stratum. Even by day, the organisms were more abundant in the shallow stratum, but at night this tendency was accentuated. This distribution in the upper water layers may be related to the partiality of Themisto for relatively high temperatures as previously mentioned.

BREEDING AND GROWTH

Young specimens appeared in the tows during January 1940, and June 1941, but numbers were comparatively few and no length frequencies were recorded. Breeding may possibly take place during summer when no cruises were made. Bigelow (1926) found young stages in the Gulf of Maine during every month from February to October, and adults with eggs at two stations on the western section of Georges Bank in July. Fish & Johnson (1937) state that rich tows of breeding Themisto were made on the northeast section of Georges Bank in September 1932. It may be assumed, therefore, that on Georges Bank breeding of Themisto takes place during summer.

PONTOGENIA INERMIS

OCCURRENCES

At one station on Georges Bank, Smith & Harger (1874) took a single specimen of Pontogenia in their dredge. Rathburn (1905) reports that Pontogenia occurs from polar seas to Vineyard Sound, is very

common in the Gulf of St. Lawrence and is taken on all kinds of bottom at Mt. Desert Island from shore to 400 m. Shoemaker (1930) states that Pontogenia is very common on the coast of New England, but of much rarer occurrence on the coast of Europe. At Woods Hole (Fish 1925), it occurred from mid July to mid August, a much shorter time than did most of the other species recorded.

In the present investigation on Georges Bank for all but two cases, both with catches one per standard haul, Pontogenia was taken within the 50 m. contour by the stramin net. In 80% of the cruises, it was mainly caught on the southwest section of the Bank. Tows of more than 100 per standard haul were made chiefly in the southwest section as follows: 1 haul, September 1939; 3 hauls, January 1940; 1 haul, June 11, 1940; 2 hauls, May 1941. Hauls of more than 500 per standard haul were made twice, once each in June 1940, and in May 1941, both in the southwest section. Very few specimens were caught during March and May 1940, for in each of these cruises there was a total of five catches only with no catch having more than eight per standard haul. Average number of specimens per standard haul per cruise indicates a mid-winter minimum; a fall and spring maximum (Table 8).

Pontogenia occurs in greatest abundance on the southwest section of the bank, but numbers in contiguous areas may vary within wide limits, viz: from a maximum of 937 per standard haul to 0 per standard haul at adjacent stations.

Pontogenia, seldom taken by the plankton samplers, was always caught in the second-depth stratum whenever it did occur during day or night tows.

The present investigation produced no data concerning the breeding and growth of Pontogenia. Adults measured an average of 12 mm., which is similar to the lengths given by Sars and Shoemaker.

NEOMYSIS AMERICANA

OCCURRENCES

Although Neomysis was not reported in the plankton from Georges Bank or the Gulf of Maine by Bigelow, it has been found in large numbers in the plankton of the Bay of Fundy during April (Fish & Johnson 1937). South of Cape Cod (Bigelow & Sears 1939), it extends to Chesapeake Bay and is confined to the inshore belt of the Continental Shelf to a distance of 30 miles from land, where it persisted in approximately the same volume from February to July. In Chesapeake Bay, it was found most plentiful in December and January. At Woods Hole, Fish (1925) states that it is present from December to April, and Smith (1879) found young and adults in Vineyard Sound during April and May. Hence, north or south of Cape Cod it generally is caught in greatest abundance during winter and spring. Perhaps Neomysis was absent from Georges Bank, as noticed by Bigelow, because the plankton collection from there was largely a summer one.

In the present collection from Georges Bank, the capture of Neomysis showed that it was very rarely caught beyond the 100 m. margin of the bank, and its distribution, with four exceptions, was always within the limits of the Mixed Area (Fig. 5). Of the four cases taken outside the Mixed Area, all had less than six individuals per standard haul. Maximum abundance invariably occurred on the shallow central axis of the bank, in the southwest, center, or northeast regions with a gradual decrease in numbers towards the margins. Throughout the year, the abundance of Neomysis fluctuated from a late fall (September to January) maximum to a winter low in February or March. Large numbers again occurred during spring but subsequently decreased in June (Fig. 5). In March 1941, catches were high in contrast with those of the previous March. Larger hauls than in the preceding year were also made during April and May 1941, although June again brought reduced catches. These results may perhaps be related either to difference in physical conditions that favor the occurrence of Neomysis or to biological differences, such as a variation in the number of animals breeding, or to a combination of these factors. Moreover, no hauls were made in certain areas of the central bank during March 1940, which may also account for some of the differences observed. Indicative of variation in physical conditions may be the circumstance that during 1941 water temperatures slightly higher than the previous year's prevailed on the bank during winter (Table 1). This eddy of even slightly warmer water may have resisted dislocation by gales or by currents from the Gulf of Maine. The Mixed Area itself is somewhat more extensive in March 1941 than in March 1940. Such physical conditions may have favored the concentration of Neomysis on the central bank in the spring of 1941 (Fig. 5). The distribution of the mycidacean suggests that catches are reduced during the coldest interval of the year and a second minimum may also occur during summer, the warmest interval.

It is interesting to observe that Neomysis sometimes occurs in very large swarms on the bank. There is also greater contrast between high and low catches than in any other species studied. When the averages per standard haul are compared (Table 8), it must be kept in mind that in September 1939, or March 1941, for example, the high averages are due to one or two of these large hauls (Fig. 5).

The swarms, which usually occur on the long axis of the bank, may be found at only one or at several stations during the same cruise, either in the southwest, center or northeast regions. They are probably related to the breeding of Neomysis which will be discussed presently.

Vertical distribution of Neomysis (Tables 3, 4) shows that it is usually taken in those areas of the bank where the second-depth stratum reaches to bottom, that is, within the 75 m. contour. This illustrates good agreement between catches of the plankton sampler and the stramin net, for the net caught very few outside the 100 m. contour. No consistent vertical migration, however, is displayed. The animal's vertical movements, apparently erratic, are not

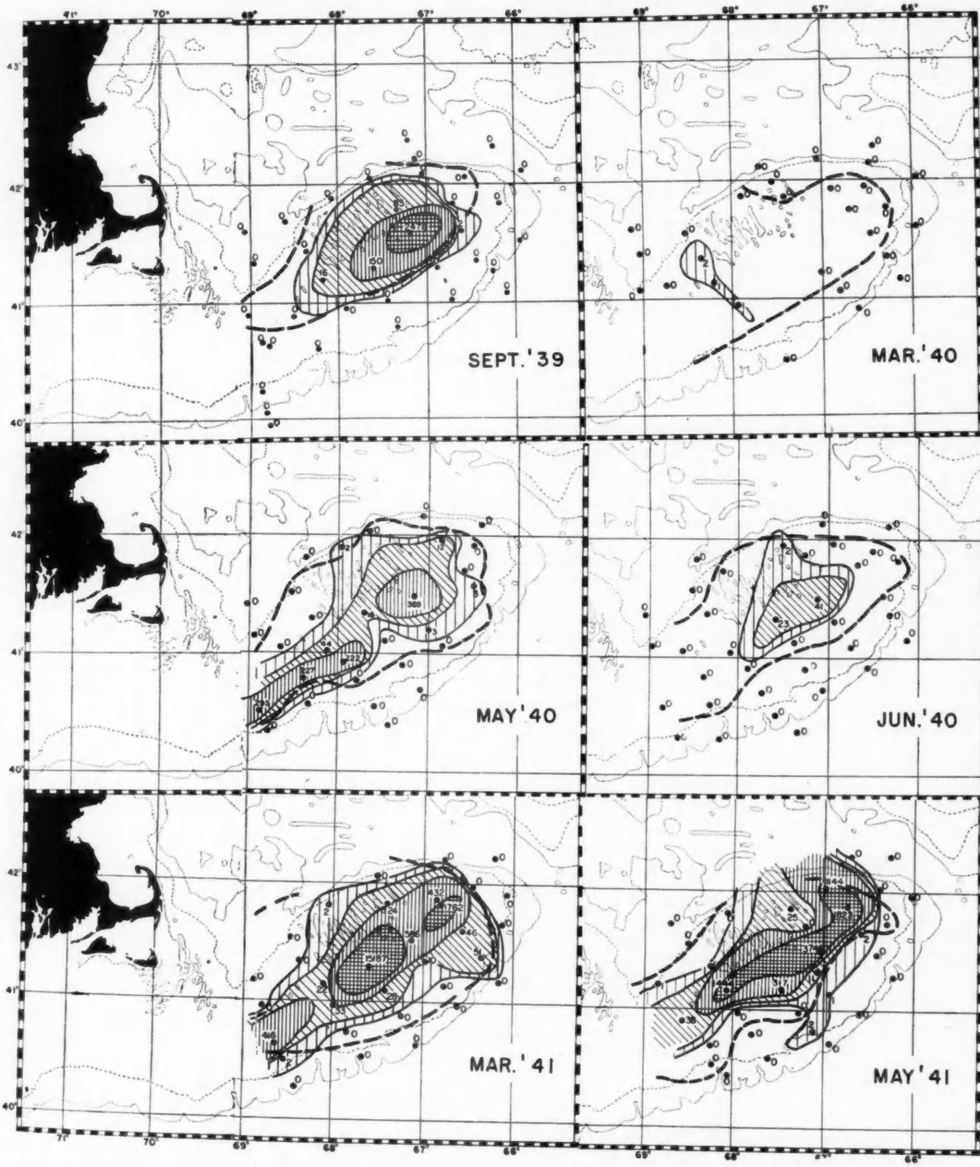

FIG. 5. Distribution of *Neomysis americana* on Georges Bank for September 1939, March, May, June, 1940; March and May 1941. Station positions designated by black dots. Numbers indicate individuals per standard haul of stramin net. Boundary of Mixed Area shown by heavy broken line.

subject to general conclusion. During daylight, greater numbers seem to be caught near bottom.

BREEDING AND GROWTH

Smith (1879) states that the breeding of Neomysis took place during spring in Long Island Sound and Casco Bay, Maine, since young and adults were taken together there during spring and summer. Smith also caught young and adults in Vineyard Sound during April and May. For *Mysis stenolepis*, a related species, Smith reports females with eggs in December in Long Island Sound and females with either empty egg sacs or carrying fully developed young in April and May.

Average length of Neomysis in the present collection was 13.4 mm. Approximately 200 individuals were measured during 1940 and little variation was

observed in adult length except that the largest individuals, up to 14-15 mm., were usually taken in May. It is perhaps regrettable that more measurements were not made either in 1940 or in 1941, but the uniformity of the catches did not then invite closer investigation of lengths. Smith (1879) gives a range of 10-12 mm. for adults in Long Island Sound, where they were commonly found in the stomachs, of shad, mackerel, herring and flounder during May.

In the Georges Bank plankton, no egg-bearing female Neomysis were observed, but in June numbers of immature mysids were caught. At least one possible breeding period is shown by the distribution data (Fig. 5). During March 1941, a large catch, 15,187 per standard haul, was made at one station. As the major portion of the catch was adults, the animals were probably swarming to breed. It is true that March 1940 (Fig. 5) does not show any similar breeding group, but on this cruise the central area was not sampled by the stramin net on account of stormy weather. Perhaps this failure to test thoroughly the bank's population may explain the marked contrast between the March results. In both years hauls of more than 1,000 per standard haul were made during the April and May cruises, and there was also a general increase in distribution on the bank as though the animals were spreading out from larger concentration centers. As this increase is a logical development in 1941, following the large March concentration, it may be assumed that a similar concentration occurred in March or early April 1940, though there is no direct evidence of it.

The data indicate, therefore, that there is probably a spring breeding period for Neomysis which in the main agrees with the findings of Smith for the New England coast.

THYSANOESSA INERMIS

OCCURRENCES

Due to its circum-polar distribution, its relatively large size (17 mm.) and the considerable numbers in which it frequently occurs, Thysanoessa plays an important role in the planktonic community of Northern seas. Euphausiid abundance in the Gulf of Maine has been noted by many investigators during the past century. Smith (1879) states that from April to October in the cold waters of Eastport, Maine, Thysanoessa and *Meganyctiphanes norvegica*, swarming on the surface "for miles," were preyed upon by schools of mackerel, pollock and immense flocks of gulls. Bigelow (1926) reported that Thysanoessa occurred more regularly over the Gulf of Maine than any other euphausiid. It was taken at 50% of the stations throughout the offshore areas though never in large numbers, but during March and April was not found on Georges Bank. Except at Eastport, it was not taken at all in the coastal zone during summer.

South of Cape Cod, Thysanoessa extends to Chesapeake Bay (Bigelow & Sears 1939) but it occurs there much less frequently than in the Gulf of Maine and always more than 30 miles from land. Smith (1879) found it abundant in Vineyard Sound during January.

In the present investigation of the plankton of Georges Bank, Thysanoessa was found to have a somewhat general distribution over the central and northern portions of the bank within the 100 m. contour during fall and winter and to disappear during summer (Fig. 6). Numbers occurring at all times were relatively small (Table 9).

Inspection of Figure 6 shows that Thysanoessa in March 1940 had only two catches of more than 50 per standard haul, these were made on the northern edge of the bank where the majority of individuals were caught in March. Few catches were made at this time on the south portion of the bank. During April 1940, there was little change in distribution, but in May even fewer catches were made in the southern and central regions, although individuals were still taken all along the north edge of the bank. In June, there was an abrupt decrease in the occurrence of adult Thysanoessa over the entire bank and catches were made only on the northern slopes beyond the 100 m. contour. Tows in September, however, showed Thysanoessa well distributed inside and outside the Mixed Area, although fewer were taken in the southern region than elsewhere. Not only in September, but also in other months the organisms seemed to occur at comparatively isolated centers of abundance on the northeast, central and northwest portions of Georges Bank (Fig. 6). For all months except September, the numbers of Thysanoessa in Figure 6 refers to adults only, as there were practically no immature stages in the other tows. Some larval stages of Thysanoessa were caught during September, however, and these were included in the September data. Stages previous to calytopis, although undoubtedly present, were not identified.

During 1941, the distribution pattern was a repetition of the previous year. Greater numbers of individuals occurred in March, however, when five tows having more than 100 per standard haul were made.

These data indicate, therefore, that while Thysanoessa does not occur in large numbers on Georges Bank, as only four tows having more than 200 per standard haul were made during all cruises, this euphausiid nevertheless has a somewhat general distribution on central and northern portions of Georges Bank from September to May.

A scrutiny of bottom temperatures (Fig. 2) shows that while Thysanoessa tends to occur in waters below 10° C., catches can be made when the bottom temperature varies from 2° C. to 16° C. Hence the occurrence of Thysanoessa undoubtedly depends on a combination of environmental factors in which temperature may be of secondary importance. The euphausiid probably tends to avoid extremes of temperature. For example, in the offshore waters of the Gulf of Maine, it is very likely present throughout the year, although it is distributed more widely during summer than in winter, indicating that sections are then unfavorable. However, it is never

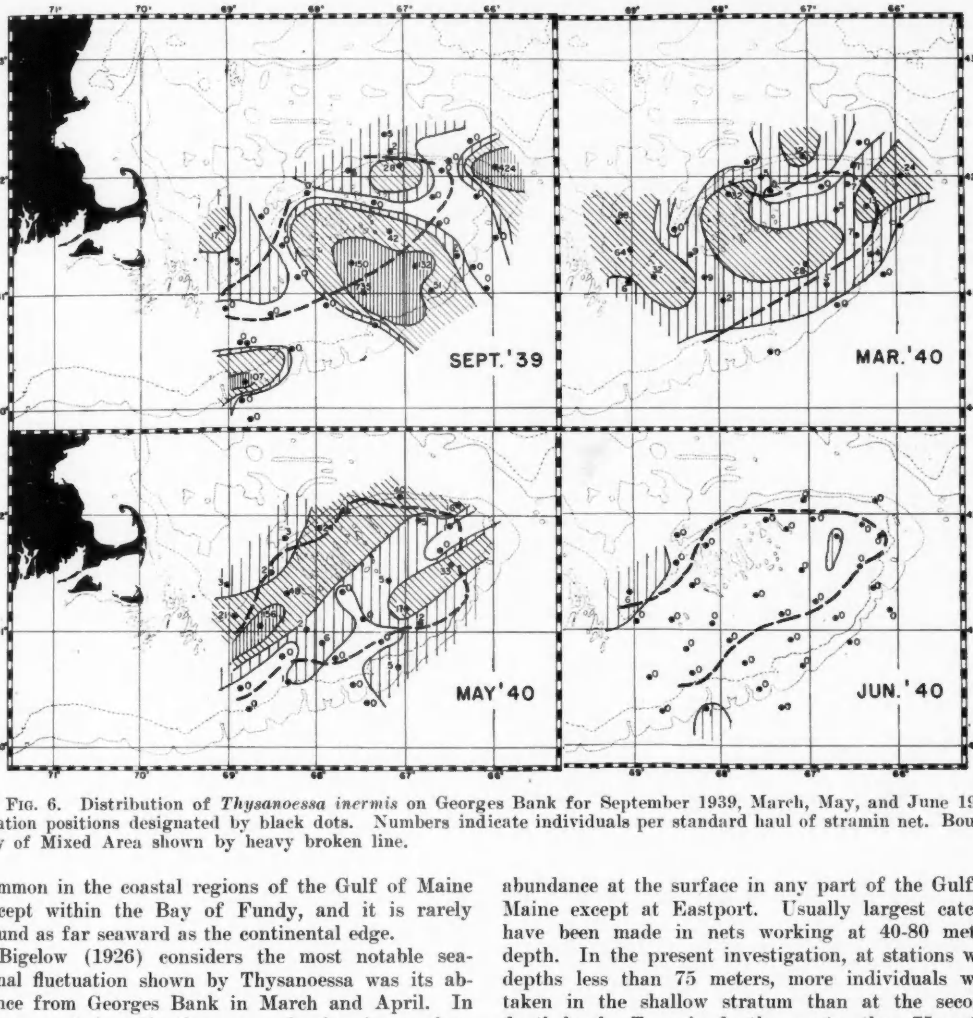

FIG. 6. Distribution of *Thysanoessa inermis* on Georges Bank for September 1939, March, May, and June 1940. Station positions designated by black dots. Numbers indicate individuals per standard haul of stramin net. Boundary of Mixed Area shown by heavy broken line.

common in the coastal regions of the Gulf of Maine except within the Bay of Fundy, and it is rarely found as far seaward as the continental edge.

Bigelow (1926) considers the most notable seasonal fluctuation shown by Thysanoessa was its absence from Georges Bank in March and April. In the present investigation, no reduction in numbers was noticed during March or April in either 1940 or 1941, but each year there was a definite disappearance of adults during June. The animals may have died after breeding or migrated from the bank to avoid an unfavorable physical environment, but since water temperatures in June are generally lower than they are in September when Thysanoessa occurs on the bank, stimulus to migrate is evidently not one solely concerned with water temperature. If the animals lack ability to make extensive horizontal migrations, their presence or absence on the bank will be chiefly influenced by prevailing currents. Possible effect of these currents on the distribution of the Crustacea will be analyzed in a subsequent discussion.

Regarding the vertical distribution of Thysanoessa, Fish & Johnson (1937) found that catches in the Bay of Fundy were largest at night. Other observers agree that this organism has never been found in abundance at the surface in any part of the Gulf of Maine except at Eastport. Usually largest catches have been made in nets working at 40-80 meters depth. In the present investigation, at stations with depths less than 75 meters, more individuals were taken in the shallow stratum than at the second-depth level. Tows in depths greater than 75 meters found the animals in the second-depth or in the deep stratum. There was some tendency for Thysanoessa to rise to the surface at night, although at depths less than 75 meters, individuals were caught in the shallow stratum equally well during day or night. Tables 3 and 4 illustrate this vertical distribution of Thysanoessa.

BREEDING AND GROWTH

Within the Bay of Fundy, Fish & Johnson (1937) found Thysanoessa breeding during March and April (eggs and nauplii) and the May tows showed a 300% increase in the number of juvenile stages of euphausiids (Thysanoessa and Meganyctiphanes) as compared with previous months. There appeared to be for Thysanoessa in this area only one breeding period ending in late June. Fish & Johnson also considered that Thysanoessa passed the win-

ter in post larval stages and matured with rising temperatures in the following spring. Bigelow (1926) reported young (unidentified) euphausiids abundant during August in the Gulf of Maine.

In the present investigation, eight egg-bearing females were caught in the March 1940 tows on the northeast part of the bank. Large numbers of euphausiid larvae were found in June. Undoubtedly these young stages are chiefly juvenile Thysanoessa as a subsequent discussion of them and of the breeding habits of the other euphausiid, ***Meganyctiphanes norvegica,*** will indicate. The appearence of these larvae may explain, perhaps, the abrupt decrease in the number of adult Thysanoessa at the beginning of summer (Fig. 6). The probability of a single annual brood of Thysanoessa in the Gulf of Maine has already been mentioned. Hence the following life cycle may occur on Georges Bank: adults breed during spring and with the onset of summer either the major portion die after breeding or are dispersed by changes in the physical environment. Adults, at any rate, disappear from the catches and Thysanoessa on Georges Bank is now represented only by the juveniles which occur abundantly in the summer tows.

Thysanoessa at various stages of growth were measured in 1939 and in 1940. In the September 1939 cruise most of the individuals in the collection appeared to be immature (Table 11). There was a gradual increase in average length from September 1939 to May 1940 as the brood reached maturity. In June 1940, evidence of what may be a new brood appears in the length-frequencies. Average length of 17.0 mm. in May indicates that a majority of the adults are mature. The length of mature Thysanoessa has been given as 17-19 mm. (Hansen 1915, Lebour 1926).

TABLE 11. Length frequency distribution of *Thysanoessa inermis* 1939-1940.

Date	Length in mm.																			Average
	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	
September 1939	..	5	1	9	2	7	7	4	5	..	..	..	..	..	..	..	..	..	..	13.3
January 1940	..	..	..	10	..	1	4	18	28	3	4	1	..	..	..	..	..	..	..	14.0
March 1940	3	..	..	24	3	14	10	30	134	45	87	21	6	12	..	1	..	..	1	15.3
April 1940	..	..	..	5	..	5	..	..	17	2	16	15	..	16	..	1	..	..	..	16.6
May 1940	..	..	..	..	..	..	..	..	14	18	39	52	6	69	..	..	..	..	..	17.1
June 1940	3	4	1	..	..	2	..	..	4	..	9	..	1	8	..	1	..	..	..	16.0

At all events the data indicates that breeding of Thysanoessa on Georges Bank may take place during spring. It is assumed that the larvae develop during summer and winter and mature during the following spring when water temperatures rise.

MEGANYCTIPHANES NORVEGICA

OCCURRENCES

Meganyctiphanes, the largest euphausiid in our plankton collection and one of the most numerous and economically important euphausiids of northern seas, on both sides of the Atlantic, has been regularly found throughout the year by many investigators in the deeper waters of the Gulf of Maine. It usually occurs outside the 100 m. contour, within the central basin of the Gulf of Maine, but depth of water by itself is apparently no bar to its distribution as it has been taken in shoal areas (Bigelow 1926, Fish & Johnson 1937). Bigelow states "it does not swarm in great numbers in the Gulf except in the northeast part where hauls indicated as many as 275 per square meter of sea surface." On Georges Bank, however, Meganyctiphanes was only taken twice by Bigelow, a fact which he is at lost to explain as there was nothing in the physical state of the water there to account for its absence.

In the present investigation of Georges Bank, Meganyctiphanes was taken inside the 100 m. contour of the bank in winter and spring on four occasions only. That is to say, during the eleven cruises, Meganyctiphanes was almost completely absent from the major portion of the bank in these seasons. However, the euphausiid was then regularly caught outside the 100 m. contour and in deeper water beyond the 200 m. contour, on both north and south edges.

Inspection of Figure 7 will show the distribution of Meganyctiphanes for several winter and spring cruises. The catches were consistently larger on the northern side of the bank where the spring maximum of 280 per standard haul was made. For both years, however, during spring only nine hauls exceeded 100 per standard haul, showing that Meganyctiphanes does not at this season have the numerical strength of such forms as *Monoculodes edwardsi* or *Neomysis americana.*

The results of the September 1939 cruise, however, show a completely different picture. Meganyctiphanes was then widely distributed both inside and outside the Mixed Area. Although nine catches of more than 100 per standard haul were made, i.e., as many as in all the other cruises added together, the large swarms were nevertheless rather scattered about the bank. Largest catches again were made beyond the 100 m. contour; the maximum was as high as 1175 per standard haul at a station just beyond the 200 m. contour off the northeast tip. Average numbers per standard haul per cruise (Table 8) show little seasonal fluctuation except for September.

Hence, it seems obvious that under certain conditions Meganyctiphanes can occur in moderate abundance on Georges Bank. It is odd that Bigelow found no Meganyctiphanes in the September plankton from this region. September 1939 chart (Fig. 7) shows, however, that on the northeast end of the bank, where the *Grampus's* stations were made, Meganyctiphanes was least plentiful inside the 100 m. line. If this condition is characteristic of the region, the *Grampus* could possibly have missed finding them there.

Distribution of Meganyctiphanes just described may suggest that the low temperatures on the bank during winter are unfavorable for the occurrence of

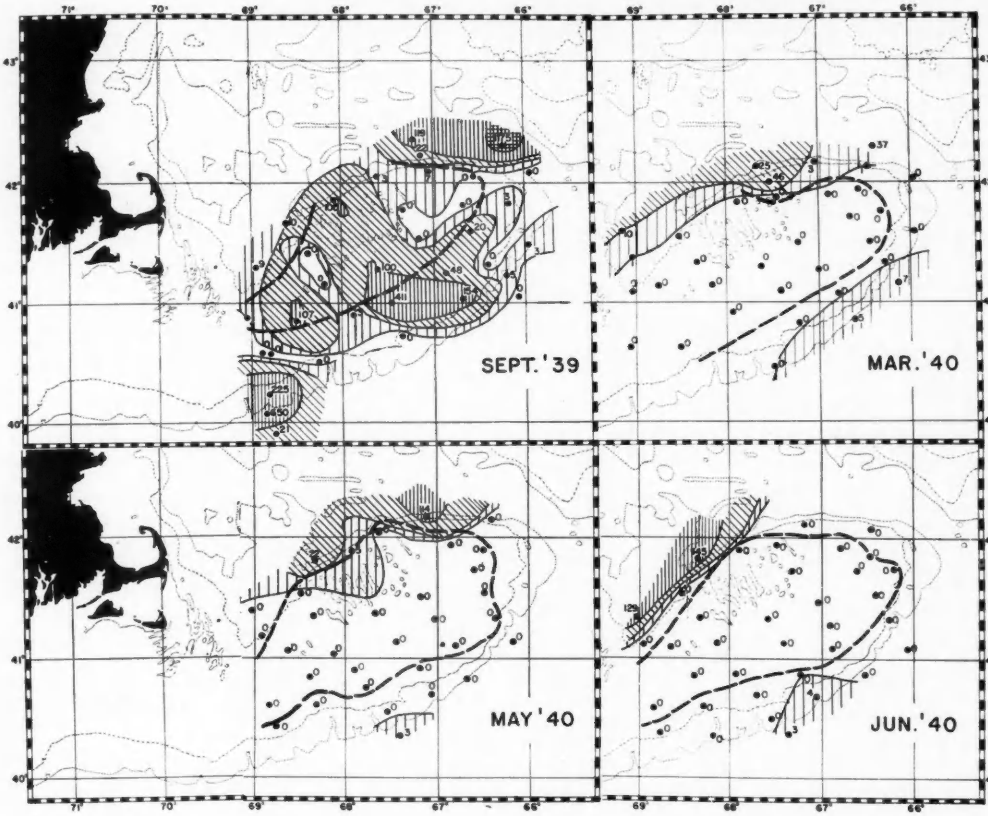

FIG. 7. Distribution of *Meganyctiphanes norvegica* on Georges Bank for September 1939, March, May, and June 1940. Station positions designated by black dots. Numbers indicate individuals per standard haul of stramin net. Boundary of Mixed Area shown by heavy broken line.

this euphausiid; but if comparison is made between the bottom temperatures on the bank (Fig. 2) and the distribution of Meganyctiphanes (Fig. 7), the organism was at times caught when the temperatures ranged from 3° C. to 16° C. If a specific cruise is selected, for example, March, 1940, which shows the coldest average temperature of the year, Meganyctiphanes was caught at stations with bottom temperatures from 3° C. to 11° C. During the April and the May cruises when the organism was caught in cool 5° water on the north side of the bank and warm (11°) water on the south side, the main portion itself had temperatures between those extremes, but in spite of these apparently suitable conditions no Meganyctiphanes were found there.

Observers have also noted that Meganyctiphanes tolerated a wide range of salinity, from 29-34 per mille, so that the slight seasonal changes on Georges Bank from 32-33 per mille would have no limiting effect on its occurrence.

It would appear, therefore, as Bigelow suggested, that other factors in addition to the physical state of the water must govern the distribution of Meganyctiphanes on Georges Bank. The most important of these factors is undoubtedly currents, the effect of which will be subsequently discussed.

As previously mentioned for *Thysanoessa inermis,* with which it frequently occurs, Maganyctiphanes is not usually caught on the surface in the Gulf of Maine except at Eastport and other parts of the Bay of Fundy. All observers agree that the normal habitat of Meganyctiphanes is in the moderate temperature and reduced light of the deeper strata, but it may as Bigelow (1926) states, "rise to the surface at any time either by the action of active vertical currents or in pursuit of food."

The vertical distribution of Meganyctiphanes in the recent cruises to Georges Bank shows that it can be caught at night equally well in both shallow and second depth strata (Table 4). In June 1940, however, on the cruise selected for the investigation of vertical distribution, Meganyctiphanes was caught only at night, even at stations beyond the 100 m. and 200 m. contours where organisms would be most likely to occur; thus the animals successfully avoided the sampler during day or else were very close to

bottom and escaped on that account. However, records not included in Table 4 show that when caught in daylight, Meganyctiphanes was usually at deep or second-depth levels. Thus there appears to be a tendency for Meganyctiphanes to rise into the shallow stratum during the night; although Bigelow (1926) considered that its appearance at the actual surface was independent of the time of day.

BREEDING AND GROWTH

In the waters of the English Channel to which it comes to breed from the deeper parts of adjoining seas, Lebour (1926) found female Meganyctiphanes with eggs and also eggs in cleavage stages in the plankton during late winter and spring.

Fish & Johnson (1937) reported eggs and larvae of Meganyctiphanes abundant in the tows at different parts of the Bay of Fundy from May to August. Meganyctiphanes usually began breeding in the spring a few weeks later than *Thysanoessa inermis* but Meganyctiphanes also had an August spawning at that time. This breeding was less extensive than during spring. Fish & Johnson also considered that at least a part of the Meganyctiphanes population of the Bay of Fundy probably survived a second year, as there were adults 35 mm. in length in November when the younger adults were not yet 24 mm.

No attempt has yet been made in the present investigation to study eggs other than those of fishes, nor has differentiation of the euphausiid larvae been attempted; but a preliminary study of the June 1940 tows failed to show conspicuous number of Meganyctiphanes larvae in them. Adult Meganyctiphanes were absent from the greater portion of the bank during spring but were invariably present along the margin. Distribution of euphausiid larvae (Fig. 9) indicates that considerable hatching had been in progress on or near the bank during May and June 1940. Conditions were similar in 1941. Hence we believe that while the larvae may be chiefly *Thysanoessa inermis,* the most numerous euphausiid on the bank during spring, young stages of Meganyctiphanes must also have contributed to the collection since adults are always present on the periphery of the bank. Little direct evidence, however, is available concerning the breeding of Meganyctiphanes on or near Georges Bank.

Length-frequency measurements were made of juveniles and adult Meganyctiphanes for some of the cruises, and the average lengths were as follows:

Cruise	*Minimum*	*Maximum*	*Average Length*
Sept. 1939	7	30	13.8 mm.
March 1940	10	35	24.1 mm.
April 1940	10	32	21.5 mm.
May 1940	10	35	24.9 mm.
June 1, 1940	10	35	24.3 mm.
June 11, 1940	15	35	25.5 mm.

The largest Meganyctiphanes caught by Hansen (1915) in deep water south of Georges Bank was 35 mm. Average length of adult Meganyctiphanes given by several authors is 25 mm. The brood of the same year thus appears to be present in the vicinity of Georges Bank from September to June. These Meganyctiphanes, as previously suggested, are not most likely to be the result of bank spawning, if indeed such breeding occurs at all, but have probably come from the Gulf of Maine or waters to the south of the bank. The occurrence of adults 30 mm. in length supports the view of Fish & Johnson that the old stock of Meganyctiphanes is not wholly replaced but survives a second year. Since there were few large adults of this size, however, the evidence is rather inconclusive.

It may be concluded that Meganyctiphanes is rarely found on the central Georges Bank area except during autumn when widely scattered centers of abundance occur. The bank appears to have little or no egg production itself. With the exception of the September catches, there is little evidence of young stages in the tows. Nevertheless, breeding of Meganyctiphanes must have taken place near the bank in the months preceding September in order to produce 13 mm. juveniles in that month. It is doubtful whether breeding takes place on the bank; hence the population must have been recruited from marginal areas. Consequently, Meganyctiphanes on the bank during September are probably migrants which will either be borne away by movements in the water mass during winter, or having increased in size and swimming ability they may become capable of retreating from unfavorable physical conditions. Bigelow (1926) considered Meganyctiphanes much less tolerant of cold water than *Thysanoessa inermis* and stated that the winter contraction of Meganyctiphanes into the deeper portions of the Gulf of Maine probably begins in October. Thus the seasonable distribution of Meganyctiphanes of Georges Bank may be partly a function of temperature, but other less obvious factors are also undoubtedly important.

CRAGO SEPTEMSPINOSUS

OCCURRENCES

Crago septemspinosus is commonly found on the North American Atlantic coast from eastern Florida to Baffin Bay and may occur from shallow water to 450 meters on all kinds of bottom. Verril & Smith (1873) found Crago to be an important item in the food of fish in Vineyard Sound. This decapod is usually collected by a bottom dredge but has been taken by tow net (Sumner, Osburn, and Cole 1911; Fish 1925). On Georges Bank, it was often reported by Smith & Harger (1874) and was usually a "common" or "abundant" species in their dredge. Egg-bearing females have been reported common in Vineyard Sound throughout summer, and young stages have been taken from April to December at Woods Hole (Fish 1925). Bigelow & Sears (1939) state that south of Cape Cod, Crago, while never abundant, was more often caught during February and April than during June and July, which suggests that it rises (or is swept upward) from the ocean floor in significant numbers most commonly during winter when turbulent movements of water are most active.

In the present investigation, Crago was distributed

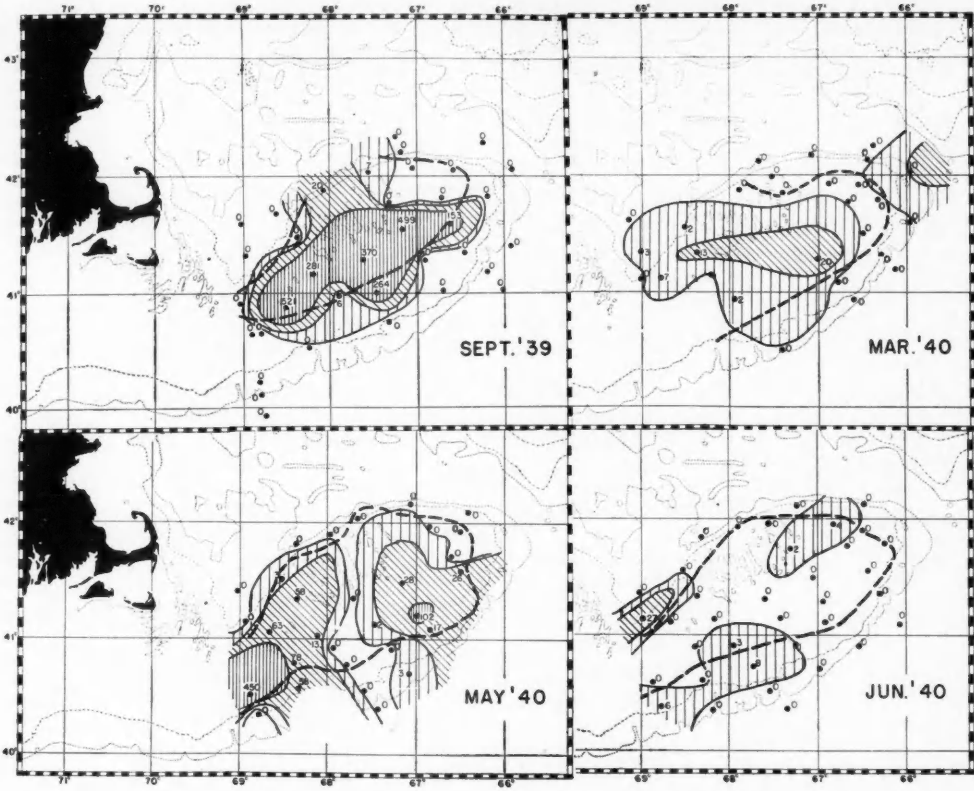

FIG. 8. Distribution of *Crago septemspinosus* of Georges Bank for September 1939, March, May, and June 1940. Station positions designated by black dots. Numbers indicate individuals per standard haul of stramin net. Boundary of Mixed Area shown by heavy broken line.

over Georges Bank with a fair degree of regularity during all eleven cruises. Concentrations were richest during September and January, poorest in June (Fig. 8). Distribution in 1941 was similar, and in neither year is there any indication of the stock being recruited from the gulf or offshore. Catches were made both inside and outside the mixed area, but with few exceptions were always made inside the 100 m. contour of the bank, either because in deeper water the net did not reach near enough to bottom or the animals do not occur on the slope. With respect to numbers occurring in the tows, there were 2 hauls of more than 100 per standard haul in May, 6 in September and 3 in January. These aggregations may be associated with the breeding habits of the organism and will be discussed in a later paragraph.

Study of the vertical migration of Crago showed that although it was seldom caught by the plankton samplers, catches were more frequently made at the second-depth and deep stratum than in the shallow stratum. Time of day had no appreciable effect on the catches.

BREEDING AND GROWTH

The following averages were obtained from the measurements of individuals during several of the cruises:

Cruise	*Minimum*	*Maximum*	*Average Length*
89 Sept. 1939	5	20	11.4 mm.
93 Jan. 1940	7	27	17.0 mm.
96 April 1940	7	35	20.1 mm.
97 May 1940	10	30	20.1 mm.

References in the literature to length of Crago are rare. Rathburn (1882) states, "some adults from southern New England equal two inches in length (51 mm.) but the average length is much lower than this." Length of 60 mm. are, however, common for this decapod in Alaskan waters (M. J. Rathburn 1904).

Length-frequencies of Crago caught on the September 1939 cruise to Georges Bank show that these were chiefly immature individuals (Table 12). Needler (1941) found that the first post-larval or bottom stages measured about 40 mm. in length. It is presumed that Crago reaches maturity within a year,

TABLE 12. Length frequency distribution of *Crago septemspinosus* in millimeters, 1939-1940.

Month	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	35	Average
Sept.	1	7	31	20	10	36	9	16	8	7	13	3	8	2	2	2	...	...	...	...	...	...	...	...	...	...	...	11.4
Jan.	...	...	1	2	10	14	8	8	5	18	19	16	24	20	19	10	13	11	4	2	8	...	1	...	...	...	...	17.0
April	...	...	...	...	...	7	3	2	1	2	3	4	5	8	12	18	10	9	14	10	6	4	8	4	...	5	1	20.1
May	...	...	...	...	...	1	2	1	1	2	6	2	4	9	11	12	10	8	6	4	5	1	2	1	1	3	...	20.1

since egg-bearing females measuring 20 to 25 mm. in length commonly occurred in our early spring catches. Length-frequencies of individuals caught throughout the year on Georges Bank show no tendency to form even a bimodal pattern, although a life span of three years has been reported for some related groups, such as the Pacific Coast Pandalidae (Needler 1930). Separate groups of larger Crago representing older year-broods may congregate on the slopes of Georges Bank as do certain pandalids on the bank slopes of the Pacific Coast; such groups of Crago the stramin net may have failed to sample. During eleven cruises, however, our catches om Crago were invariably made inside the 100 m. contour. Obviously, in the present investigation, insufficient evidence permits no definite conclusions concerning the length of survival or maximum growth of Crago on Georges Bank, although data indicate a single annual brood which agrees with the findings of Fish & Johnson (1937).

Maximum numbers of juvenile Crago were taken in July at Woods Hole and during August in the Bay of Fundy where they were the most abundant benthonic larvae in the tows (Fish 1925, Fish & Johnson 1937). In the Gulf of St. Lawrence, breeding occurs from mid-June through July (Needler 1941).

The first egg-bearing females were observed in the Georges Bank tows during April 1940, others occurred in May and June. Many decapod larvae were caught in the May and June tows. These facts suggest that on Georges Bank, breeding of Crago probably begins during spring and continues into early summer. South of Cape Cod, Bigelow & Sears (1939) found in late June off New York that young stages of Crago occurred in mid-depth in such abundance as to be an important item in the general planktonic community. In the present investigation, the decapod larvae were not identified and will be discussed as a group later, but there is reason to believe that a large proportion of the decapod larvae found in the May and June tows on Georges Bank were juvenile Crago.

DICHELOPANDULUS LEPTOCERUS

OCCURRENCES

Dichelopandulus was the largest species of crustacean in our plankton collection from Georges Bank. This decapod has a wide distribution ranging along the northeast Atlantic Coast from eastern Long Island to Greenland. Less abundant south of Cape Cod than north of it, catches of Dichelopandulus in the Gulf of Maine have been reported where occasionally "more than a peck were caught in a single haul of the beam trawl" (Rathburn 1882). Presumably this was the result of one hour's tow. Rathburn states that Dichelopandulus associated with other species of shrimps, must have occurred in "immense shoals" in the Gulf of Maine as very large hauls were sometimes made, but on account of the activity of the animals such large catches were difficult to secure consistently. Dichelopandulus was reported "common" in several dredge hauls on Georges Bank by Smith & Harger (1874).

The distribution of Dichelopandulus on Georges Bank as determined by the present investigation showed that either the shrimp were scarce or the stramin net failed to catch them at the majority of stations. Catches were usually made on or near the 100 m. line and, with the exception of the South Channel region where some always occurred, were irregularly distributed from cruise to cruise along this contour. Only in September 1939 were any of these decapods caught on the central bank area. Greatest number of catches for any cruise was nine and the least four. The average catch per standard haul per cruise, based only on stations where the organism occurred, varied between 5 and 6 per standard haul, except for September 1939, when an average of 42 per standard haul was obtained. This higher average was chiefly the result of one haul, a catch of 172 per standard haul made on the central bank. Even if this catch is omitted, however, the resulting average of 23 per standard haul is still higher than the average of the other cruises. Hence greater numbers of Dichelopandulus appear to be on the bank in September. This abundance may be connected with the organism's reproductive cycle and will be discussed in a later paragraph.

Concerning the vertical distribution of Dichelopandulus little information is provided by the plankton sampler catches because this decapod rarely occured in them. Catches that were made were taken in the second-depth or deep stratum irrespective of time of day.

BREEDING AND GROWTH

During September the population of Dichelopandulus sampled by the stramin net was obviously composed of both juveniles and adults (Table 13). This September cruise is the only one which so clearly shows such a mixture of age-groups. The shrimp caught in succeeding months all appear to belong to one brood. The presence of large numbers of young as well as older individuals in September is probably responsible for the several large hauls in the month which, as previously mentioned, swelled the September average catch far above that of the other cruises.

TABLE 13. Length frequency distribution of *Dichelopandulus leptocerus* in millimeters 1939-1940.

Month	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	32	34	35	36	38	40	45	50	55	60	Average
September	5	1	12	10	4	20	3	19	4	4	3	..	4	4	2	4	1	..	2	..	6	1	1	1	..	1	..	1	2	1	1	19.3
March	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	8	..	..	1	..	4	..	2	..	..	..	..	1	1	..	..	30.5
April	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	6	..	..	..	2	12	..	3	6	..	..	3	..	..	..	3	34.8
May	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	2	2	3	2	..	47.0
June 11	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	..	1	..	1	3	1	7	2	..	46.5

Rathburn (1882) reported Dichelopandulus up to 100 mm. in length from Massachusetts Bay. No individuals of this size were taken during the present investigation, however, although egg-bearing females 55-60 mm. in length were caught during May and June 11, 1940. Rathburn stated that egg-bearing females (size not given) were caught during August and September in Massachusetts Bay. Hence, although little direct evidence of breeding was found, the presence of both egg-bearing females in May and June and numerous small immature specimens in September indicated that Dichelopandulus very probably breeds during summer on Georges Bank. Had cruises been made during summer perhaps additional evidence would have been obtained.

Concerning the life-cycle of Dichelopandulus little further is known. Length-frequency distribution (Table 13) does not suggest a series of year-groups, but insufficient individuals may have been measured to demonstrate adequately this possibility. The pandalidae of the British Columbia coast, such as *Pandulus danae* and *Pandulus borealis* (adult length, 100-150 mm.) have been found to live for at least three years, and become mature in the autumn of the second year as males then reverse their sex to bear eggs in the third year (Needler 1930). The adults are only found in quantity beyond 100 meters although smaller specimens are found in the shoaler water.

Should Dichelopandulus have a life-cycle somewhat similar to these decapods the major portion of Georges Bank may be too shallow for the large adults. Most of the catches made on the bank were taken near the 100 meter contour, except those of the younger ones in September which occurred chiefly on the shallow central bank. As the animals increased in size they may have withdrawn from the main bank to the deeper slopes more favorable to adult life, and the stramin net would probably have failed to catch adults living close to bottom near the 200 meter contour. Nevertheless, the immature stages found in September may have been due partly to the breeding of such adults or they may have developed from larvae which had drifted on to the bank from the South Channel area or from Massachusetts Bay where large individuals have been caught in the past by Rathburn and others.

Although available data to support these conjectures is insufficient, the possibility is suggested that Dichelopandulus is the largest and longest-living crustacean in our collection from Georges Bank.

SCHIZOPODA IMMATURE

OCCURRENCES

When the tows were first examined and the organisms counted immature mysidae and euphausiid larvae were grouped together for, until the June cruises, very few occurred in the tows. Although mysids leave the marsupial pouch with a full complement of appendages and are in all important characters like the adult, whereas euphausiids go through a series of larval stages following their leaving the egg as a nauplius, the two groups were formerly classified as Schizopoda. In this present paper the immature mysidae and the euphausiid larvae have not been separated; they have for convenience been designated Schizopoda Immature, as the term although obsolete exactly describes in this particular case the organism under discussion. It may be noted, however, that the immature mysidae appeared less abundant than the euphausiid larvae.

Relatively few (one or two hauls per cruise) of the immature Schizopoda were taken by the stramin net from September to April. Hauls taken were made along the south or northeast edges of the bank, either near the 100 meter contour or in the deeper water beyond the 200 meter line. No hauls were made on the north edge or on the central bank during this autumn and winter period. With the approach of spring and extending into summer there was a distinct change in occurrence (Fig. 9). Catches per standard haul increased considerably during May 1940. In May, 1941 the increase was even greater and the distribution more widespread. During June in both years large numbers of individuals were caught all along the south margin of the bank and were also found in the west and north areas inside the 100 meter contour. In June, 1940 there were 15 catches of more than 100 per standard haul and one of more than 1000 per standard haul. Even greater numbers occurred during June 1941 when there were 20 catches of more than 100 per standard haul and 10 of more than 1000 per standard haul. In other respects the distribution of immature Schizopoda in 1941 followed the previous year closely. Hence the abundance of these organisms is, as far as our records show, minimal during autumn and winter; greatest during early summer.

In May, when the first marked increase in immature Schizopoda occurred, organisms were caught in greatest numbers beyond the 200 m. line on the south edge of the bank. They were entirely absent from the central bank until late June. Therefore, it would

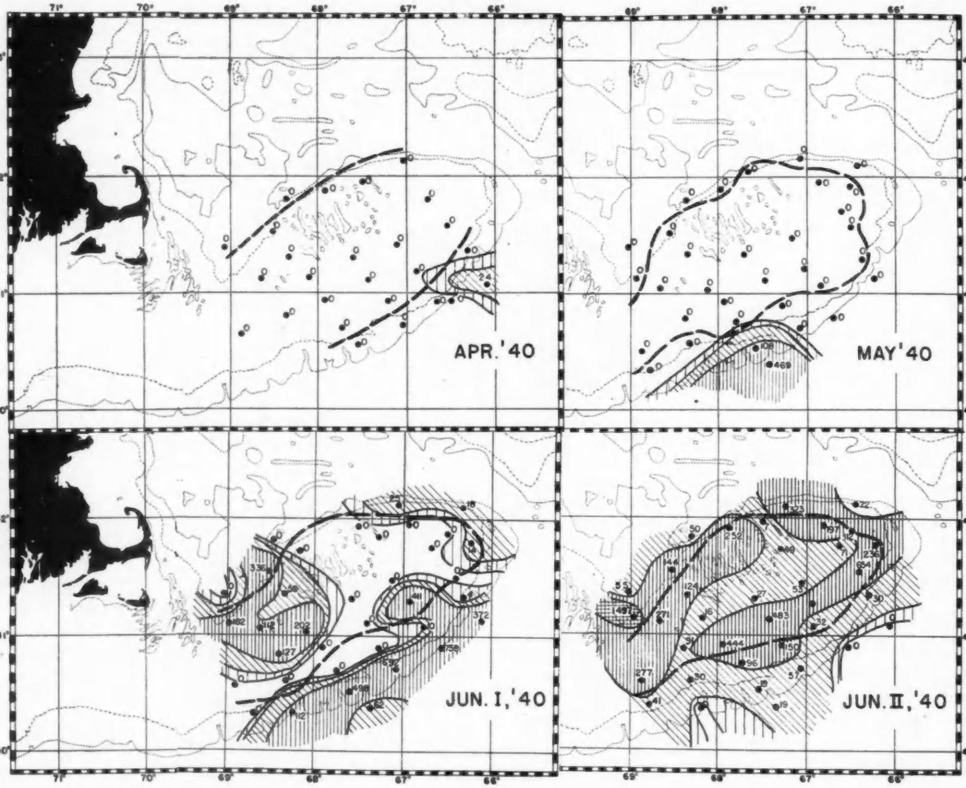

FIG. 9. Distribution of immature Schizopoda on Georges Bank for April, May and both early and late June cruises in 1940. Station positions designated by black dots. Numbers indicate individuals per standard haul of stramin net. Boundary of Mixed Area shown by heavy broken line.

appear that adults contributing, for example, to the May and June collections, were breeding in deep water beyond the 200 m. margin of the bank. The distribution and breeding of *Neomysis americana* have already been discussed. From March to May, Neomysis occurred on the central regions always inside the 100 m. contour. Numbers decreased in June; increased again in September (Fig. 5). Obviously Neomysis did not contribute to the early spring collections of immature Schizopoda. The June catches, however, may have been influenced by breeding Neomysis. In June 1941, large numbers of immature Schizopoda were caught in the southwest region where big catches of adult Neomysis had occurred from March to May. *Erythrops erythrophthalma* was the only other mysid in the Georges Bank plankton and its occurrence was sporadic. It was, however, always found beyond the 100 m. contour of the bank and usually beyond the 200 m. contour; hence, it may have contributed immature mysides to the March and April offshore catches.

The most abundant euphausiid in the Georges Bank plankton was *Thysanoessa inermis*. As previously discussed, adults were found on the bank during spring but disappeared with the onset of summer, either to avoid unfavorable physical conditions or because currents which might affect their distribution changed in strength. There is evidence that Thysanoessa breeds during spring; hence some of the large numbers of euphausiid larvae which occurred in the immature Schizopoda collection probably resulted from the breeding of this euphausiid. Few immature Schizopoda were caught in September, but many late calytopis stages of euphausiids and small, immature Thysanoessa were caught during this month. It is very doubtful that *Meganyctiphanes norvegica* breeds successfully on Georges Bank, for reasons previously mentioned, but it has a wide distribution in the gulf and occurs on the seaward slopes, hence the facts seem to indicate that while *Meganyctiphanes norvegica* and *Erythrops erythrophthalma* may contribute chiefly to the slope catches and *Neomysis americana* to the June central bank catches, immature Schizopoda on the bank are chiefly composed to juvenile *Thysanoessa inermis*. If this assumption is correct, then although adult Thysanoessa disappears in June, the animal does not fail to be

represented as a species on Georges Bank throughout the year. The adults may be absent but eggs and larvae remain to develop on the bank.

The vertical distribution of immature Schizopoda, shown by the plankton sampler catches, demonstrates that the animals occur most frequently in the second-depth stratum, although there is a tendency for them to migrate into the shallow stratum at night.

DECAPOD LARVAE

OCCURRENCES

On Georges Bank, decapod larvae were caught during January in very few tows and in small quantities. There was a decided increase in size of catches with the onset of spring (3 hauls of more than 500 per standard haul in May) but the occurrence of the larvae did not begin to increase sharply until June when they were taken at 22 stations, approximately twice as many as in May (Fig. 10). Results similar to these were found for the waters south of Cape Cod by Bigelow & Sears (1938). On Georges Bank, the larvae occurred chiefly within the 100 m. contour and many catches were made on the central area of the bank.

The larvae, characteristically concentrated in April and May when several catches of more than 1000 per standard haul were made, had become more evenly distributed by June when approximately 50% of the hauls were more than 100 per standard haul. This increase in average abundance suggests that by chance the spring tows had been made in areas where considerable hatching had previously taken place, and that in the meantime dispersal of the larval swarms had been accomplished, probably by the action of currents or other water movements. Wide fluctuation in numbers is a common characteristic of the occurrence of decapod larvae during spring. Throughout summer, decapod larvae undoubtedly occur on Georges Bank in considerable numbers since, when compared with June, the September catches indicated no reduction in quantity or extent of distribution.

Because egg-bearing *Crago septemspinosus* have been observed in May and June on Georges Bank, many of the decapod larvae in the Georges Bank collection can be attributed to this species. Late larval stages of Crago were identified in the plankton but no estimate of their number was taken. Several investigators have noted in New England and Canadian waters the abundance of *Crago septemspinosus* larvae in the plankton during summer (Bigelow

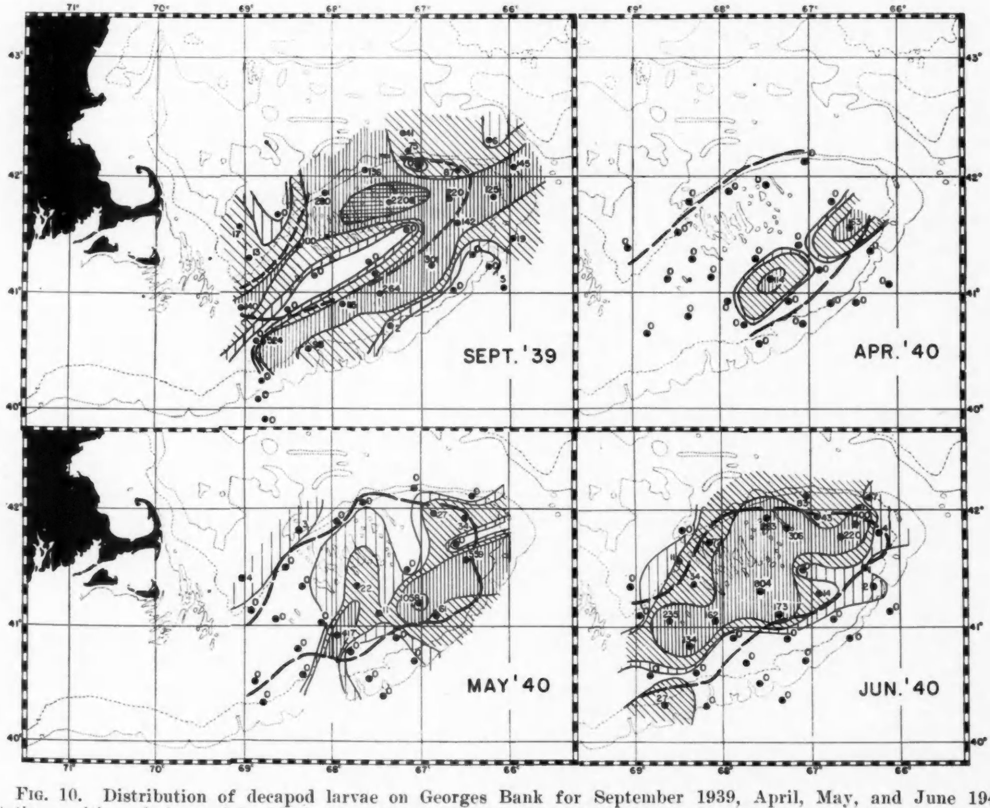

FIG. 10. Distribution of decapod larvae on Georges Bank for September 1939, April, May, and June 1940. Station positions designated by black dots. Numbers indicate individuals per standard haul of the stramin net. Boundary of Mixed Area shown by heavy broken line.

1926, Fish & Johnson 1937; Bigelow & Spears 1939). Other decapods, however, such as several species of rock and hermit crabs are also known to live on Georges Bank and their larval stages also occur in the plankton (Smith & Harger 1874, Bigelow 1926). The larvae of crabs and other decapods have been reported to provide rich food for mackerel on Georges Bank (Kendall 1908).

Vertical distribution of decapod larvae caught by plankton sampler indicates that the crustaceans occur chiefly in the shallow stratum, although there is a slight tendency for them to sink into the second-depth stratum at night.

To conclude, a number of decapods probably contribute to the decapod larvae of Georges Bank. The larvae are found chiefly within the 100 m. contour of the bank and usually the largest catches are made on the central area. The larvae occur on the bank in considerable numbers throughout late spring, summer and fall, but are greatly diminished in occurrence during winter.

DISCUSSION

The larger crustacea of Georges Bank dealt with in this paper have been shown to be planktonic, at least during part of their life, hence their distribution will be affected in varying degrees by water movements. Redfield (1939) states "the geographical distribution of organisms in the sea is a hydrodynamic problem." The environment of specific regions will be determined by a complex balance of physical and biological factors. Of these factors flow of water is one of major importance affecting both the nature of the environment and the supply of organisms to it. The present knowledge of the physical oceanography of Georges Bank is limited because as yet, no satisfactory method of observing the complex and often sudden changes in such shallow water areas has been perfected. Ecological studies by biologists of animal communities within the Gulf of Maine and Georges Bank have contributed to the knowledge of the current systems of these areas (Redfield 1939, Clarke, Pierce, and Bumpus 1943), but for this purpose the larger Crustacea may be less satisfactory, since on the one hand, their swimming powers may not be as feeble as is usually supposed, and on the other, they may at times rest on the bottom and fail to indicate water movements there.

It is important to keep in mind that "bank" water is a mixture of Gulf of Maine and oceanic water and that the process of mixing is continuous although the rate may vary.

During summer Georges Bank is relatively well-stirred but is surrounded by more stable stratified water. There is little flow of water across the bank from the Gulf of Maine at this time since the peripheral current around the north and east margins is strong. Stability of the stratified layers surrounding the bank and also over the bank is probably at its maximum in September, hence vertical turbulence must be greatly suppressed compared to other seasons. Relatively heavy, saline water may be drawn up on the bank from seaward and pumped along its bottom, as it were, by each successive tidal wave. This water is mixed slowly with lighter, fresher water drawn into the central eddy from the Gulf of Maine. Mixed water would concurrently drain off the bank at different levels. These water movements may set in motion subsidiary eddies or counter currents.

For the colder months of the year little is known about the bank's circulation. Persistence of the population of *Sagitta elegans* throughout winter has been considered an index of permanence for at least part of the bubble of Mixed Area water (Clarke, Pierce, & Bumpus, 1943). Dynamic isobaths calculated by Watson (Redfield 1940, Fig. 10) suggest that as temperature falls with the onset of winter, contrast between bank water and the surrounding water masses may be so reduced that between January and March the peripheral current around the bank, formed by the Gulf of Maine eddy, practically disappears and Gulf of Maine water sweeps freely across Georges Bank. Isobaths are widely spaced for January showing that such water movement is slow. Heavy winter gales may have a dislocating effect on this type of water, forcing masses of it off shore. Although Iselin (1939) states that local gradient currents must be greatly reduced before winds can have marked effect, otherwise bank or coastal water would be blown seaward much more often than it is. During March and April isobaths indicate a slackening flow across the bank and gradual reestablishment of the peripheral current. Bigelow (1926) found the whole area of Georges Bank "dead water" in March. Presumably, as spring is succeeded by early summer, velocity and volume of the bank's peripheral current increases due to progressive incorporation of river water into the northwestern sides of the Gulf. Since water no longer flows across the bank lateral components again become more important factors in the mixing mechanism.

Thus there may be two phases, as it were, in the cycle of the mixing mechanism. During winter vertical turbulence is the predominant factor at work, but in summer and autumn when stability of the strafied layers is high, turbulence of this type is restricted to shoal areas and lateral mixing of water becomes the more important factor.

Distribution of *Monoculodes edwardsi, Neomysis americana* and *Crago septemspinosus* (Figs. 3, 5, 8) demonstrates that these organisms were present on Georges Bank throughout the eleven cruises. Failure to catch *Neomysis americana* in March 1940 as compared with March 1941 (Fig. 5) can be explained only by assuming either the organisms had perished for some reason or they were in a very localized swarm on the central bank which the March survey did not sample. Swarms of this type encountered in January and April, 1940 lend plausibility to such an assumption.

During spring, while numbers of individuals of these three species had decreased, their distribution

in the water mass remained about the same as before. Decline in relative numbers was probably due more to normal mortality, or to tidal mixing distributing the population more homogeneously than to dislocation of the water mass and its animal population by currents or gales. For, if the latter were the case, marked differences in distribution would likely result. Numbers of each species decreased towards the 200 meter contour, which indicates that the bank was not receiving additions to its stock from Gulf or offshore. Hence, occurrence of these species, which as adults are characteristic of bottom water, is thus either independent of currents set up by the mixing process or the movement of bottom water is too gradual to disperse them. Friction undoubtedly affects motion of bottom water and tends to increase its permanence.

Additional evidence for the permanence of at least certain layers of Georges Bank water is suggested by the development of *Thysanoessa inermis* and *Crago septemspinosus*. September catches of these crustaceans were composed chiefly of young stages, while January to March catches showed a steady increase in length of individuals (Tables 11, 12). These data show the same population of *Thysanoessa inermis* and *Crago septemspinosus* continued on the bank during fall and winter. Moreover, individuals from broods off the bank did not appear to have been introduced. Distribution of *Monoculodes edwardsi* and *Crago septemspinosus* indicated that extensive horizontal water movements or eddies in the bottom water of Georges Bank might be formed, nevertheless. There was no close similarity in the distribution of these two organisms for most of the year, beyond that already mentioned, but during spring in 1940 and 1941 both were unusual in having certain common features; the horizontal occurrence during April and May appeared to change from an irregular pattern to one with a well defined east and west group separated by an area having few or no individuals (Figs. 3, 8). These eddies may be associated with the initiation in spring of active lateral mixing.

History of the population of *Meganyctiphanes norvegica* and *Themisto compressa* during winter was different from any of the other crustaceans discussed inasmuch as these organisms were not found on Georges Bank at that season. Meganyctiphanes, relatively widespread in September, had disappeared from Georges Bank by January and was subsequently caught only at deep stations on the bank slopes (Fig. 7). Additional evidence for the general occurrence of adult Meganyctiphanes in the Gulf adjacent to Georges Bank was provided by tows made with a continuous plankton recorder (Hardy 1946). Beyond the 200 meter contour Meganyctiphanes was the only large crustacean caught by the recorder along the entire northern edge from March to June. Because Meganyctiphanes disappeared so completely during winter they were either swept away by flow of water across the bank, or they had then developed the ability to swim actively enough to avoid unfavorable environmental conditions, or they perished as a result of such conditions. Displacement of Meganyctiphanes, at least up to January, would not appear likely, at any rate *Themisto compressa* showed no sign of decrease at that time. Indeed, absence of adults of both species during winter and spring could hardly be attributed to water movement alone since the organisms were endemic to Gulf of Maine and bank slopes and at least some of those swept on and off the bank would be caught there. Available data, nevertheless, pointed to their absence. The physical state of the water that presented an unfavorable environment may have been responsible for their nonoccurrence. Several ecological factors were also undoubtedly involved, however, since, as already has been mentioned, the organisms were often caught only on the slopes during spring when comparable conditions existed on the central bank itself. Therefore, while temperature by itself may have been a limiting factor at certain extremes, a combination of influences, as yet imperfectly understood, probably affect the organism's distribution during winter and spring on Georges Bank.

To conclude, the characteristics and distribution of these species: *Monoculodes edwardsi*, *Crago septemspinosus*, and *Neomysis americana* indicate an endemic existence for them on Georges Bank. There was no evidence that the organisms were being carried to the bank from the surrounding areas. Individuals, bred in spring, maintain the bank population at a high level as adults through autumn and winter. Reduction in numbers is the normal result of mortality rather than loss by water movement. Hence bottom layers of water on Georges Bank appear to have considerable permanence even during winter, a season when the practically homogeneous water mass is most likely to be dislocated by gales or other dynamic agencies.

On the other hand occurrence during autumn of *Themisto compressa*, and *Meganyctiphanes norvegica*, animals endemic to Gulf and water surrounding the bank, contributes evidence for a mixing of water over the bank. In the stable, stratified layers surrounding it, the Georges Bank's mixing action may form frictional eddies or currents by which water is drawn towards the central mass of mixed water. The large numbers of immature animals of these species carried, apparently, by this inflowing water may have been drawn from Gulf of Maine and slope stocks by lateral turbulence. Absence during winter and spring of these organisms is believed due either to ability of adults to avoid in some way the drift to the bank and the unfavorable conditions which may exist there or they are carried to the bank only to perish quickly. Species such as *Themisto compressa* and *Meganyctiphanes norvegica* occur on Georges Bank, therefore, only as migrants. There is no evidence of local stocks.

Distribution and characteristics of *Thysanoessa inermis* suggest that it is intermediate between the endemic forms and the migrants. Water movements or physical conditions that disperse *Themisto compressa* or *Meganyctiphanes norvegica* do not affect it during late autumn and winter. Moreover, its dis-

tribution in March and April indicates *Thysanoessa inermis* may be circulating in eddies that have no obvious influence on the other two groups. Withdrawal of *Thysanoessa inermis* with the onset of summer has no clear relationship to flow of water off Georges Bank, inasmuch as the peripheral current is now well established around it. Hence, absence of *Thysanoessa inermis* in summer may be due either to death of adults after breeding or to withdrawal of the organisms from an unfavorable environment. Distribution of *Thysanoessa inermis* as compared with the other larger crustaceans emphasizes the individual differences that may exist among plankton of Georges Bank.

Distribution of *Sagitta elegans* studied by Clarke, Pierce, & Bumpus indicated that very small amounts of water were entering the Mixed Area from the south and east in September, whereas distribution of *Thysanoessa inermis, Meganyctiphanes norvegica* and *Themisto compressa* demonstrates either that lateral components were then contributing to the mixing mechanism or that these animals were reacting to a favorable environment and entering it by their own efforts. It is actually possible that both influences were at work. In the sagittae investigation it was also found that a tongue of water rich in Calanus, extending across the eastern end of Georges Bank and curving south, was a clear indication that a current from the Gulf was flowing over the southern margin of the bank. Distribution of *Themisto compressa* seems to check more closely with the probable path of this current than does the distribution of *Thysanoessa inermis* and *Meganyctiphanes norvegica.* Hence this current is probably surface water.

Thus, occurrences of the larger crustaceans on Georges Bank illustrate the complex relationships and varied character of the ecological factors governing distribution of animals on the bank. Possible effect of currents set up by the mixing mechanism on the distribution of several organisms have been described, yet it is realized that currents are baffling and elusive forces since they often change strength and direction with changing depth and are also affected by varying turbulence of wind. Techniques for measuring these changes have not yet been perfected. The effect of water temperature on distribution is also not entirely clear. The conclusions stated are suggested with these limitations in mind in the hope that they may serve a useful purpose in furthering the ecological study of Georges Bank.

SUMMARY

1. Assuming that 300 cubic meters of water was filtered during the standard haul of a stramin net, the range in average volumes of crustacean plankton on Georges Bank varied from a March-April minimum of 0.1 cc. per cubic meter to a June maximum of 0.6 cc. per cubic meter. Both maximum average volumes and maximum individual volumes occurred in June. Maximum individual catch was 1200 cc. per standard haul or approximately 4.0 cc. per cubic meter. These average volumes of plankton caught by the stramin net were found to compare favorably with more complete measurements of plankton made elsewhere on both sides of the Atlantic. Hence it is clear that Georges Bank supports a rich plankton.

2. Mackerel, herring, cod, and other commercially important fishes were shown to depend on the larger crustaceans or their larvae for much of their food. These crustaceans have therefore an important role in the food cycle of Georges Bank.

3. Tows from the region forming the long axis of the bank had the greatest volumes of plankton on all cruises. Presumably a number of factors, such as; type of bottom, moderate depth and physical state of the water, a rich and prolonged supply of phytoplankton (Sears 1941) combined to produce on this extensive area lying between the northern shoals and the 100 meter contour to the south an environment favorable for the breeding of the larger crustaceans.

4. Of the larger planktonic crustaceans on Georges Bank the predominating organisms in the stramin net collection were; *Monoculodes edwardsi, Themisto compressa, Pontogenia inermis Neomysis americana, Thysanoessa inermis, Meganyctiphanes norvegica, Crago septemspinosus, Dichelopandulus leptocerus,* Schizopoda immature, decapod larvae.

5. With the exception of *Meganyctiphanes norvegica* and *Dichelopandulus leptocerus* the crustaceans were usually caught inside the 100 meter contour of the bank.

6. The amphipod *Monoculodes edwardsi* showed the greatest average abundance and widest distribution of all the species in the plankton collection. It was taken at approximately 60% of the hauls and of all species had the highest average number per standard haul per cruise for seven of the eleven cruises.

7. The species next most widely distributed and generally abundant were *Crago septemspinosus* and *Meganyctiphanes norvegica,* which occurred in not less than 10% of all hauls and had an average of one or more per standard haul for each cruise.

8. *Neomysis americana* occurred in the largest swarms but showed marked fluctuations in abundance. Individual catches up to 15,000 per standard haul were made when in adjacent areas under apparently similar physical conditions catches were small.

9. Although never occurring in the plankton as abundantly as the mysid *Neomysis americana* or the amphipod *Monoculodes edwardsi,* the large size and bulk of the euphausiids *Thysanoessa inermis* and *Meganyctiphanes norvegica* or the decapods *Crago septemspinosus* and *Dichelopandulus leptocerus* must be considered in order to estimate their true role in the food cycle of the bank. Each of these crustaceans would be approximately four to six times the size of the previously mentioned smaller species.

10. A seasonal variation in occurrence was shown by *Pontogenia inermis, Themisto compressa,* decapod larvae, Schizopoda immature which were caught most frequently during spring and summer; *Thysanoessa inermis,* during autumn and winter; *Meganycti-*

phanes norvegica and *Dichelopandulus leptocerus*, during autumn. *Neomysis americana* avoided both the coldest and the warmest periods of the year.

11. Breeding during spring and summer was common for many of the larger planktonic crustaceans. *Thysanoessa inermis* and *Neomysis americana*, however, probably bred only during spring; while *Meganyctiphanes norvegica* presumably did not breed at all on the bank.

12. With the possible exception of *Dichelopandulus leptocerus*, which may live three years, the larger crustaceans are believed to have a one year life-cycle.

13. Vertical distribution of the organisms showed that the majority were caught in the second depth stratum, with the exception of *Thysanoessa inermis* and *Themisto compressa* caught more often in the shallow stratum, though not necessarily on the shoal areas of the bank.

14. *Monoculodes edwardsi, Thysanoessa inermis*, and *Meganyctiphanes norvegica* showed some tendency to move into the shallow stratum at night. *Meganyctiphanes norvegica* was never taken in the shallow stratum by day, the other two species were sometimes caught there equally well by day or night. There was no other marked vertical migration during day or night.

15. Many of the larger crustacea were caught both inside and outside the Mixed Area. They therefore tolerate a moderately broad range of temperatures and salinities. Species largely confined within the Mixed Area were *Pontogenia inermis*, caught where temperature varied from 5° C. to 10° C., and *Neomysis americana*, which preferred a 4° C. to 5° C. temperature range. Concerning the effect on distribution of variations in food supply or the nature of the bottom little at present is known.

16. Invariably caught outside the Mixed Area were *Meganyctiphanes norvegica* and *Dichelopandulus leptocerus*. *Meganyctiphanes norvegica*, while a creature of the banks on both sides of the Atlantic, usually withdrew from extremes of temperature or salinity. Apparently it avoided areas having temperatures below 3° C. and above 16° C. *Dichelopandulus leptocerus* appeared to be a benthonic decapod that preferred cold water.

17. Distribution of *Monoculodes edwardsi, Neomysis americana* and *Crago septemspinosus* on Georges Bank showed them to be endemic there, thus indicating that the deep stratum, irrespective of the boundaries of the Mixed Area, could have permanence during winter and spring, although extensive eddies might occur in it. This finding is an extension of the suggestion of Clarke, Pierce, & Bumpus that the homogeneous water on Georges Bank may have permanence from season to season.

18. Distribution of *Thysanoessa inermis* indicated that young stages either hatched from local spawning or else drifted to the bank during spring and summer. Adults present during winter months were absent in spring. They may have died after breeding or have been dispersed by changes in the physical environment. Water movement was not obviously an important limiting factor. *Themisto compressa* and *Meganyctiphanes norvegica* also appeared to be migrants, drifting as juveniles to central Georges Bank in late summer and autumn. Adults were caught only on the bank's margin during winter and spring.

REFERENCES

Bigelow, H. B. 1926. Plankton of the offshore waters of the Gulf of Maine. Bull. U. S. Bur. Fish. **40**(2): 1-509.

Bigelow, H. B., & Mary Sears. 1939. Studies of the waters of the continental shelf, Cape Cod to Chesapeake Bay III. A volumetric study of the zooplankton. Mem. Mus. Comp. Zool. **54**(4): 183-378.

Bigelow, H. B., & W. C. Schroeder. 1939. Notes on the fauna above mud bottom in deep water in the Gulf of Maine. Biol. Bull. **76**(3): 303-324.

Clarke, G. L., E. L. Pierce & Dean Bumpus. 1943. The distribution and reproduction of Sagitta elegans on Georges Bank in relation to the hydrographical conditions. Biol. Bull. **85**(3): 201-226.

Dunbar, M. J. 1945. On Themisto Libellula in Baffin Land coastal waters. J. Fish. Research. Bd. Canada. **6**(6): 419-434.

Edwards, G. A., & L. Irving. 1943. The influence of temperature and season upon the oxygen consumption of the sand crab, Emerita talpoida. J. Cell. and Comp. Physiol. **21**(2): 169-182.

1943. The influence of season and temperature upon the oxygen consumption of the beach flea, Talorchestra megalopthalma. J. Cell. and Comp. Physiol. **21**(2): 183-189.

Einarsson, H. 1945. Euphausiacea. Dana Rept. **27:** 1-185.

Ewing, M., A. Vine, & J. Worzel. 1946. Photography of the ocean bottom. Jour. Optical Soc. Amer. **36**(6): 307-321.

Ewing, M., G. P. Wollard, A. Vine & J. Worzel. 1946. Recent results in submarine geophysics. Bull. Geol. Soc. of Amer. **57**(10): 909-934.

Fish, C. J., & M. Johnson. 1937. The biology of the zooplankton population in the Bay of Fundy and Gulf of Maine with special reference to production and distribution. Jour. Biol. Bd. Can. **3**(3): 189-321.

Fish, C. J. 1925. Seasonal distribution of the plankton of the Woods Hole region. Bull. Bur. Fish. **41:** 91-179.

Hansen, H. J. 1915. The Crustacea Euphausiacea of the U. S. National Museum. Proc. U. S. Nat. Museum. **48:** 59-114.

Hardy, A. C. 1936. The Continuous Plankton Recorder. Discovery Repts. **11:** 457-553.

Holmes, S. J. 1901. Phototaxis in the Amphipoda. Amer. Jour. Physiol. **5**(4): 211-234.

1903. Sex recognition among Amphipods. Biol. Bull. **5**(5): 288-292.

1903. Synopses of North American Invertebrates, The Amphipoda. Amer. Nat. **37:** 267-292.

1905. The Amphipoda of southern New England. Bull. U. S. Bur. Fish. **24:** 459-529.

Iselin, C. O'D. 1939. Some physical factors which may influence the productivity of New England's coastal waters. Sears Found. Jour. Mar. Res. **2:** 74-85.

Kunkel, B. W. 1918. Arthrostraca of Connecticut. Bull. Nat. Hist. Survey of Conn. **26:** 1-261.

Lebour, Marie V. 1926. The Euphausiidae in the neighborhood of Plymouth. Thysanoessa inermis. Jour. Mar. Biol. Assoc. **14**(1): 1-21.

Needler, A. B. 1930. The Post-Embryonic Development of the common Pandalids of British Columbia. Contrib. Can. Biol. **6**(6): 81-163.

1930. Migrations of haddock and the interrelationships of haddock populations in North American waters. Contr. Can. Biol. Fish **6**(10): 243-313.

1941. Larval stages of Crago septemspinosus. Trans. Roy. Can. Inst. **23**(50): 193-199.

Parr, A. E. 1936. On the probable relationship between vertical stability and later mixing processes. Journal du Conseil, **11**(3): 308-313.

Rathburn, Mary J. 1904. Decapod crustaceans of the Northwest Coast of North America. Smithson. Inst. Harriman Alaska Expedition. **10**: 1-337.

1905. Fauna of New England, Crustacea. Occa. Papers Boston Soc. Nat. Hist. **7**(5): 1-117.

1929. Canadian Atlantic Fauna. 10 Arthropoda Decapoda. Biol. Bd. Canada **10**: 1-38.

Rathburn, Richard. 1882. Notes on the shrimp and prawn fisheries of the United States. Bull. U. S. Fish Comm. **2**: 139-152.

Redfield, A. C. 1939. The history of a population of Limacina retroversa during its drift across the Gulf of Maine. Biol. Bull. **76**: 26-47.

1940. Factors determining the distribution of populations of Chaetognaths in the Gulf of Maine. Biol. Bull. **79**: 459-487.

Sumner, F. B., R. C. Osborn & Leon J. Cole. 1913. A biological survey of the waters of Woods Hole and vicinity. Bull. U. S. Bur. Fish. **31**(2): 547-794.

Smith, S. I., & A. E. Verril. 1874. Invertebrate animals of Vineyard Sound. Rept. U. S. Fish Comm. 295-478.

Smith, S. I. 1879. The stalkeyed crustaceans of the Atlantic coast of North America, north of Cape Cod. Trans. Conn. Acad. **5**: 27-138.

Smith, S., & O. Harger. 1874. Report on the dredgings in the region of St. Georges Banks in 1872. Trans. Conn. Acad. **3**(1): 1-64.

Skutch, A. 1926. Habits and ecology of tube building Amphipods. Ecology, **7**: 481-502.

Sars, G. O. 1895. An account of the Crustacea of Norway. **1**: 1-711.

Shoemaker, D. R. 1930. Amphipoda of the Cheticamp Expedition of 1917. Contr. Can. Biol. **5**(10): 221-359.

Stephensen, K. 1924. Report Danish Ocean. Exped. **2**(D-4): 71-149.

Smallwood, M. E. 1905. The salt march amphipod Orchestra palustris. Cold Spring Harbour Monograph. **3**: 3-23.

Zimmer, Carl. 1909. Die Nordischen Schizopoden. Nordisches Plankton **6**: 1-178.

EXPERIMENTAL STUDIES OF INTERSPECIES COMPETITION

I. COMPETITION BETWEEN POPULATIONS OF THE FLOUR BEETLES, *TRIBOLIUM CONFUSUM* DUVAL AND *TRIBOLIUM CASTANEUM* HERBST

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EXPERIMENTAL STUDIES OF INTERSPECIES COMPETITION

1. COMPETITION BETWEEN POPULATIONS OF THE FLOUR BEETLES, *TRIBOLIUM CONFUSUM* DUVAL AND *TRIBOLIUM CASTANEUM* HERBST

INTRODUCTION

There is much speculation and some fact in ecological and evolutionary literature about competition between populations which are brought into tension with each other through their respective demands upon an environment shared by both but limited in its potentialities for exploitation. It is usually agreed by common consent that this problem is biologically significant; that it is complex in character and difficult to analyze, and that it merits active investigation in the field, the laboratory, and through stochastic processes.

A creditable start has been made along this line of ecological research. There is a considerable literature dealing with natural and experimental populations and with various theoretical aspects. Because of the recent publication (1947) of Crombie's valuable review devoted to the general topic, however, it is not necessary to discuss these papers here and the reader is referred to this source and papers by Elton (1946) and Williams (1947) for orientation.

The present study is designed to explore and describe what happens when two closely related species of flour beetles, *Tribolium confusum* Duval and *Tribolium castaneum* Herbst, are placed into direct competition in a shared environment to which both are individually well adapted. Tribolium seems particularly favorable for research of this type. Much is already known of its population behavior. It lends itself to laboratory manipulation and to accurate census. Its environment, flour, is not a synthetic but a natural environment. Further, there seems to be some theoretical meaning in using two species of the same genus instead of selecting forms of greater taxonomic divergence. The cogency of the last point was recognized by Charles Darwin who, in Chapter III of *The Origin of Species*, wrote, "As the species of the same genus usually have, though by no means invariably, much similarity in habits and constitution, and always in structure, the struggle will generally be more severe between them, if they come into competition with each other, than between the species of distinct genera."

The experiments shortly to be discussed have been rather broadly conceived and extensively carried out, both as to their duration and replication. It is considered desirable in any study of competition, whether field or laboratory, to observe the populations long enough so that a judgment can be reached about their eventual equilibria, and in sufficient numbers, so that variability within cultures of similar design and between cultures of dissimilar design can be statistically appraised. While these desiderata are not completely satisfied in every case reported here, as much has been done over the four-year period as time and facilities have permitted. Because the data raise more problems than they solve, this paper is to be considered primarily as descriptive in scope and not definitive. To signify the point that future research is needed and may be anticipated, a new series of publications is inaugurated herewith under the title "Experimental Studies of Interspecies Competition" of which this is the first contribution.

It is a privilege to acknowledge the assistance of a number of friends and colleagues who have aided me immeasurably in the conduct of this research and in the preparation of the manuscript. I am greatly indebted to Doctor Lowell J. Reed, Vice-President of the Johns Hopkins University and Professor of Biostatistics at that institution, for taking time from a busy schedule to discuss the data after the computations had been made. This conference was most stimulating and helpful. Professor Sewall Wright, of the University of Chicago, offered several cogent suggestions. Mr. L. C. Birch, of the University of Sydney, and Marian Burton Frank, of the University of Chicago, read the manuscript much to its profit. Doctor Clay G Huff, of the Naval Medical Research Center, generously assisted me with matters pertaining to the identification and life-cycle of the parasite *Adelina tribolii*. Doctor A. C. Crombie, of Cambridge University, loaned me a typescript copy of his important manuscript on interspecies competition in advance of its publication (1947). Mr. David Lack, of Oxford University, offered several stimulating suggestions when he was a visitor in this laboratory. Doctor Asher J. Finkel, of the University of Chicago, discussed with me certain segments of the data. Joan Barnes contributed greatly by her skillful and meticulous drafting of the figures. Finally, I am sincerely grateful to the following associates who at various times assisted untiringly in the exacting and laborious tasks of counting so many thousands of beetles and in keeping the laboratory routines in smooth working order: Marion Biggs Davis, Nina Leopold Elder, Marian Burton Frank, Virginia Miller Gregg, Shirley Horwitz, and Catharine Lutherman Kollros.

MATERIALS AND METHODS

Census Procedures

The technical procedures followed in this study were designed to satisfy three general requirements: to maintain the physical environment as constant as possible; to minimize and equalize handling of the beetles, and to supply the organisms with an optimal nutritive medium renewed at thirty-day intervals.

All populations were kept in dark incubators at a constant temperature of 29.5° C. (±0.5°) and at a relative humidity of 60 to 75 per cent. The medium consisted of 95 per cent whole-wheat flour sifted through No. 8 silk bolting-cloth and then fortified by the addition of dry brewer's yeast powder in the amount of five per cent by weight. To ensure homogeneity, the yeast and flour were thoroughly admixed in a mechanical rotating device. The populations were established in two sizes of glass containers and in three volumes of medium. The smallest volume (8 grams) was placed in shell vials 9.5 × 2.5 cm., and the larger volumes (40 and 80 grams) were placed in wide-mouthed bottles 10 × 7 cm.

These bottles containing the medium were then heated at 60° C., for three hours to kill any foreign organisms or parasitic cysts that might have been in the flour. Upon cooling, and before being used, they were stored for a week in an incubator in which they reach the requisite temperature and humidity equilibria of 29.5° and 60-75 per cent.

Census counts were taken at thirty-day intervals for every population regardless of its type. A census consists first in passing the infested medium through a No. 00 bolting cloth sieve that retains the imagoes, pupae, and larger larvae. These are gently brushed into a finger-bowl and, after dead forms and frass are removed, they are counted by means of a hand tally and the numbers recorded by stage categories. The finer siftings are then screened through a No. 2 bolting cloth that retains the larvae of intermediate sizes. These are placed on black paper, counted, and the number recorded. Most of the eggs are retained by this mesh (No. 2). They are carefully rolled off the black paper into the storage finger-bowl but not counted. The final sifting utilizes a No. 8 cloth that retains all eggs and the smallest larvae. The latter are counted and are placed, along with the larger stages and the eggs, into bottles containing the desired amount of fresh medium.

This method of census thus permits an accurate, *total* count to be made of all larvae, pupae, and imagoes, without any loss of eggs, and a re-establishment of the population in fresh medium for another thirty-day period. In the case of "experimental" or two-species cultures, each imago beetle is identified under the microscope as to species (i.e., either *Tribolium confusum* or *T. castaneum*) using the eye and antennal characters described and figured by Good (1936), and this essential datum is recorded.

Several comments are appropriately included here concerning fecundity, rate of metamorphosis, and imaginal longevity of the two species of flour beetles.

Fecundity

In two independent oviposition experiments, carried out several years apart in this laboratory at temperatures of 29° C. (±0.5), *T. castaneum* exhibited a significantly higher rate of fecundity than did *T. confusum*. These experiments were conducted under the relatively optimal conditions of one pair of young imago beetles in eight grams of medium with the latter renewed at regular intervals. The data merely show that a species difference in fecundity exists in a highly favorable environment. They tell nothing about oviposition under population conditions—conditions in which various degrees of crowding and competition obtain which greatly reduce egg production, as is known, and which perhaps reduce egg production differentially by species, as is not known. The last aspect has an obvious relevance for the present study and is now being investigated. Although, as indicated above, *T. castaneum* lays more eggs, there exists a rather large difference between the two species in the two assay experiments the reason for which is not understood. In one (the first conducted), *T. castaneum* had an oviposition rate, over a 60-day assay period, of 12.8 eggs per female per day as compared with 12.1 for *T. confusum*—a difference of approximately 6 per cent ($P = 0.0012$). Comparable rates for the second experiment were 14.9 for *T. castaneum* and 10.8 for *T. confusum*—a difference of approximately 28 per cent ($P < 0.0000$). Kollros (1944) studied the fecundity of *T. castaneum* using the same stocks and conditions and obtained a rate in close agreement with the last figure, namely: 13.5 eggs per female per day. Despite these divergencies it is reasonable to conclude that one species of flour beetle possesses a higher reproductive potential than the other. This datum is important for our present purposes.

Metamorphosis

Under the experimental conditions described earlier both *T. confusum* and *T. castaneum* require roughly about a month to pass through their respective post-embryonic periods which they do with negligible mortality at 29° C. *T. castaneum*, however, does this at a slightly faster pace largely by reducing the length of the egg and pupal stages. This can be summarized by reporting data presented by Kollros (1944) for *T. castaneum* and by Stanley (1946) for *T. confusum*, as follows:

	Egg stage (days)	*Larval period (days)*	*Pupal stage (days)*	*Total period (days)*
T. confusum	5.5	22.4	7.0	34.9
T. castaneum	3.8	22.8	6.2	32.8

Imago Longevity

Life tables for *Tribolium confusum* have been published by Pearl, Park, and Miner (1941), and some observations on mean life-duration of *T. castaneum* are included in the manuscript by Kollros. It seems clear that the latter species has a significantly shorter average life than does the former. Data, pertinent to this point and extracted from the two reports, are as follows (expressed as mean number of days):

	Males	Females
T. confusum	177.8 ± 2.8	198.5 ± 3.5
T. castaneum	115.6 ± 2.2	107.7 ± 2.4

These, again, are observations accumulated under favorable conditions of assay and do not necessarily represent events as they occur in populations.

Sufficient background has now been presented about the methods used in this study and about the ecological life-history and husbandry of the two species of Tribolium. Should the reader wish further orientation in such matters he is referred to the following papers: Boyce (1946), Chapman & Baird (1934), Dick (1937), Ford (1937), Good (1936), Holdaway (1932), Park (1934, 1941), and Park & Davis (1945).

THE EXPERIMENTAL DESIGN

The design of this study, patterned in part after that of Park, Gregg, and Lutherman (1941), can be clarified by reference to Table 1 from which the following points are to be noted:

(1) Three volumes of medium were used: 8 grams, designated hereafter as "I"; 40 grams, designated as "II"; and 80 grams, designated as "III."

(2) All populations were started by introducing imagoes in equal sex ratio in a density of one beetle per gram of medium. Thus, I had a total initial population of 4 males and 4 females; II, of 20 males and 20 females; and III, of 40 males and 40 females.

(3) There are "control" and "experimental" populations. The controls are single species cultures either of *T. confusum* or *T. castaneum*. The experimentals are mixed cultures in which interspecies competition is established within the ecosystem. Table 1 shows that the experimentals are started in one of three ways. First, *T. confusum* and *T. castaneum* adults are introduced in equal proportions (E-a). Second, *T. confusum* is introduced at a numerical advantage over *T. castaneum* in the proportion ¾ : ¼ (E-b). Third, *T. castaneum* is given a similar initial advantage over *T. confusum* (E-c).

(4) The table also lists total days of observation, number of replicated cases for each category,[1] and contains a code system by means of which each type of population can be readily identified. The reader is urged to memorize this code because it will be used repeatedly as the paper develops. In all instances the first notation is a Roman numeral that identifies the volume as explained above. The second notation identifies the culture as a control (C) or an experimental (E). For controls, the lower case "b" signifies a pure culture of *T. confusum;* "c" a pure culture of *T. castaneum.* For experimentals, "a" signifies that each species was introduced in a 50% ratio; "b" signifies that *T. confusum* comprised 75% of the total; and "c", that *T. castaneum* comprised 75% of the total.

(5) The bottom two rows of Table 1 refer to special populations grown under parasite-free conditions and designated "sterile" (S). These will be treated in detail later.

From the discussion of methods, and consideration of the experimental design, it should be clear that it is technically feasible to census, accurately and with negligible injury, two sorts of populations (single and competing species) cultured for long periods of time in a nutritious, regularly renewed environment of three different volumes under sufficiently constant conditions of temperature, moisture, and light.

[1] Because the taking of a census is time-consuming and laborious even for the volume I series, a practical limitation is necessarily imposed on number of replicates. Every effort has been made, however, to conduct this study utilizing as many cases as possible. It has taken approximately 40 hours a week over the four-year period to accumulate the data reported here.

TABLE 1. Design of the entire investigation.

Volume of Medium	Total Initial Imago Population	Initial Imago Density (per gram)	CONTROLS (single species)			EXPERIMENTALS (2 species in competition)			
			Code	Number of replicates at start	Total days of observation	Code	Initial ratios of imagoes at start	Number of replicates at start	Total days of observation
I (8 gm.)	8	1	I-C-b	20	1380	I-E-a	b = c(1/2:1/2)	15	780
			I-C-c	20	1380	I-E-b	b > c(3/4:1/4)	15	750
						I-E-c	b < c(1/4:3/4)	15	690
II (40 gm.)	40	1	II-C-b	17	1350	II-E-a	b = c(1/2:1/2)	9	1020
			II-C-c	18	1380	II-E-b	b > c(3/4:1/4)	7	540
						II-E-c	b < c(1/4:3/4)	7	930
III (80 gm.)	80	1	III-C-b	2	1410	III-E-a	b = c(1/2:1/2)	2	750
			III-C-c	2	1410	III-E-b	b > c(3/4:1/4)	2	360
						III-E-c	b < c(1/4:3/4)	2	810
I STERILE	8	1	I-C-b-S	20	1140	I-E-a-S	b = c(1/2:1/2)	18	840
			I-C-c-S	20	1140				

SINGLE SPECIES POPULATIONS: CONTROLS

INTRODUCTORY

Although the primary concern of this study lies in the quantitative description of what happens when *Tribolium confusum* and *Tribolium castaneum* are cultured as competing populations, it is impossible to discuss this phenomenon with cogency until there is a clear understanding as to how each species behaves when grown by itself in the absence of such competition. An effect presumed to result from competitive pressure cannot be assumed unless it is shown that this particular effect is absent in the controls. Thus it is necessary to review in detail each type of control population described in Table 1; to compare these as to species noting differences and similarities, and to make some statement about their respective variabilities. This will be developed as follows. By means of tables and graphs, populations of *T. confusum* in the three volumes are discussed first. Then, comparable data for *T. castaneum* are presented. Next, the two control groups, designated in Table 1 as "steriles," are reviewed along with a discussion of their significance for the study as a whole. Finally, the species differences between *T. confusum* and *T. castaneum* are statistically analyzed for the total period of observation and conclusions, required in the interpretation of the experimental populations, are formulated.

The basic data for all eight types of control populations are presented in Tables 2-9. Each table is similar in construction and the entries are computed in the same way, as can be illustrated by an examination of Table 2. The table lists age of the populations by 30 day intervals, these corresponding, of course, to census periods. Then, the actual number of larvae and pupae, imagoes, and their sum totals for every age is noted. These figures are derived from all replicates and expressed as mean number per gram of medium. When expressed in this way it is possible to compare directly all three volumes. The tables also contain two columns in which the larvae and pupae, and the imagoes, are reported in percentages. As will be evident later, these percentages add information of interest when *T. confusum* controls are contrasted with *T. castaneum*. The last column *(n)* lists the number of individual populations existing at any particular age, or the number of cases from which the means were computed.

TRIBOLIUM CONFUSUM CONTROLS

(I-C-B, II-C-B, III-C-B)

The data for control populations of *T. confusum* in the three volumes are tabulated in Tables 2, 3, and 4 and graphed in Figure 1. This figure, plotting mean number per gram as a logarithmic ordinate against time in days as the abscissa, presents the curves for the I, II, and III series. Each series is represented by three components: total numbers, number of imagoes, and number of larvae plus pupae (hereafter written "larvae-pupae").

From the graphs and tables it is possible to draw certain conclusions about populations of *T. confusum* kept under the particular conditions outlined in the preceding section.

In the first place the cultures maintain themselves successfully under these conditions. After 1410 days

TABLE 2. Larvae and pupae, imagoes, and sum totals for **I-C-b** over 1380 days of observation. Data are expressed as mean percentage of larvae and pupae, and imagoes, per 30-day census period and as mean number of individuals per gram of medium. (N.B. Slight discrepancies in the first decimal place exist for certain of the percentages in Tables 2 through 9 owing to the fact that these were computed before the numbers were reduced to "per gram" units).

Age (days)	LARVAE AND PUPAE		IMAGOES		Sum M/gm.	n
	M=#/INDV M/gm.	Per cent	M/gm.	Per cent		
30...	24.5	90.6	2.5	9.4	27.0	20
60...	4.1	16.8	20.5	83.2	24.6	20
90...	1.5	6.8	20.7	93.2	22.2	20
120...	1.2	5.5	20.1	94.5	21.3	20
150...	1.0	4.8	19.2	95.2	20.2	20
180...	1.4	7.4	17.6	92.6	19.0	20
210...	1.5	9.2	14.7	90.8	16.2	20
240...	4.6	27.1	12.5	72.9	17.1	20
270...	4.4	30.4	10.1	69.6	14.5	20
300...	7.6	46.4	8.8	53.6	16.4	20
330...	7.3	45.3	8.9	54.7	16.2	20
360...	8.0	47.6	8.8	52.4	16.8	20
390...	7.0	44.3	8.8	55.7	15.8	20
420...	5.9	40.7	8.6	59.3	14.5	20
450...	7.6	49.5	7.7	50.5	15.3	20
480...	6.5	44.1	8.2	55.9	14.7	20
510...	6.0	44.1	7.6	55.9	13.6	20
540...	7.9	52.1	7.3	47.9	15.2	20
570...	8.4	52.2	7.7	47.8	16.1	20
600...	7.3	47.0	8.3	53.0	15.6	20
630...	7.3	48.9	7.7	51.1	15.0	20
660...	7.2	50.2	7.1	49.8	14.3	20
690...	11.8	63.7	6.8	36.3	18.6	20
720...	11.6	62.2	7.0	37.8	18.6	20
750...	14.7	66.8	7.3	33.2	22.0	19
780...	13.3	64.6	7.3	35.4	20.6	19
810...	13.2	64.9	7.1	35.1	20.3	19
840...	12.5	64.4	6.9	35.6	19.4	19
870...	11.8	64.5	6.5	35.5	18.3	19
900...	14.9	70.2	6.3	29.8	21.2	19
930...	14.6	67.0	7.2	33.0	21.8	19
960...	13.0	61.4	8.2	38.6	21.2	19
990...	11.8	60.2	7.8	39.8	19.6	19
1020...	16.4	68.5	7.6	31.5	24.0	19
1050...	15.2	67.5	7.3	32.5	22.5	19
1080...	18.6	72.7	7.0	27.3	25.6	19
1110...	14.9	67.3	7.2	32.7	22.1	19
1140...	15.8	70.0	6.8	30.0	22.6	19
1170...	13.6	66.2	6.9	33.8	20.5	19
1200...	16.0	71.3	6.4	28.7	22.4	10
1230...	14.6	68.6	6.7	31.4	21.3	10
1260...	13.5	69.0	6.1	31.0	19.6	10
1290...	12.5	67.4	5.9	32.6	18.4	10
1320...	13.0	68.7	5.9	31.3	18.9	10
1350...	16.0	72.2	6.2	27.8	22.2	10
1380...	15.8	71.5	6.3	28.5	22.1	10

the populations are as healthy, when judged by their size and equilibria, as they were when three (or more) years younger. The reduction in number of replicates shown in the *n*-column of Tables 2 and 3 was voluntary and does not signify culture mortality.

Secondly, it is clear from Figure 1 that volume of medium imposes no differences in the pattern of growth and maintenance. The curves for I, II, and III are remarkably similar to each other along the time axis as is immediately evident from inspection of the graphs. The curves for Series III are not as smooth as are those for the smaller volumes. This

TABLE 3. Larvae and pupae, imagoes and sum totals for **II-C-b** over 1350 days of observation. Data are expressed as mean percentages of larvae and pupae and imagoes per 30-day census period and as mean number of individuals per gram of medium.

Age (days)	Larvae and Pupae M/gm.	Larvae and Pupae Per cent	Imagoes M/gm.	Imagoes Per cent	Sum M/gm.	n
30...	23.4	85.9	3.8	14.1	27.2	17
60...	4.2	15.2	23.5	84.8	27.7	17
90...	1.4	5.7	23.4	94.3	24.8	17
120...	0.6	2.7	22.8	97.3	23.4	17
150...	0.8	3.2	21.5	96.8	22.3	17
180...	1.3	6.0	19.4	94.0	20.7	17
210...	2.2	11.6	17.1	88.4	19.3	17
240...	3.9	21.5	14.1	78.5	18.0	17
270...	5.2	31.3	11.4	68.7	16.6	17
300...	6.2	39.2	9.6	60.8	15.8	17
330...	7.6	47.4	8.3	52.6	15.9	17
360...	6.9	47.1	7.9	52.9	14.8	17
390...	7.8	52.8	7.0	47.2	14.8	17
420...	8.2	55.0	6.7	45.0	14.9	17
450...	8.8	56.1	6.9	43.9	15.7	17
480...	8.8	57.4	6.6	42.6	15.4	17
510...	9.3	59.7	6.3	40.3	15.6	17
540...	9.3	59.0	6.4	41.0	15.7	17
570...	8.9	57.6	6.6	42.4	15.5	17
600...	7.3	51.8	6.8	48.2	14.1	17
630...	7.8	55.2	6.4	44.8	14.2	17
660...	9.5	61.1	6.1	38.9	15.6	17
690...	9.8	63.3	5.6	36.7	15.4	17
720...	11.3	68.8	5.1	31.2	16.4	17
750...	12.8	73.3	4.7	26.7	17.5	17
780...	12.0	73.0	4.4	27.0	16.4	17
810...	10.7	69.2	4.7	30.8	15.4	17
840...	9.9	67.1	4.9	32.9	14.8	17
870...	10.3	67.0	5.1	33.0	15.4	17
900...	10.9	68.6	5.0	31.4	15.9	17
930...	11.7	66.3	6.0	33.7	17.7	17
960...	10.9	63.0	6.4	37.0	17.3	17
990...	10.9	62.8	6.5	37.2	17.4	17
1020...	10.0	59.1	6.9	40.9	16.9	17
1050...	11.1	61.1	7.0	38.9	18.1	17
1080...	11.5	63.5	6.6	36.5	18.1	17
1110...	12.7	66.4	6.4	33.6	19.1	17
1140...	10.7	63.3	6.2	36.7	16.9	17
1170...	11.6	66.9	5.7	33.1	17.3	17
1200...	10.9	67.7	5.2	32.3	16.1	10
1230...	11.7	70.7	4.8	29.3	16.5	10
1260...	10.3	67.6	5.0	32.4	15.3	10
1290...	10.9	68.8	4.9	31.2	15.8	10
1320...	10.1	63.8	5.7	36.2	15.8	10
1350...	11.4	65.1	6.1	34.9	17.5	10

TABLE 4. Larvae and pupae, imagoes, and sum totals for **III-C-b** over 1410 days of observation. Data are expressed as mean percentage of larvae and pupae and imagoes per 30-day census period and as mean number of individuals per gram of medium.

Age (days)	Larvae and Pupae M/gm.	Larvae and Pupae Per cent	Imagoes M/gm.	Imagoes Per cent	Sum M/gm.	n
30...	22.0	89.5	2.6	10.5	24.6	2
60...	2.2	9.4	21.1	90.6	23.3	2
90...	0.6	2.6	20.9	97.4	21.5	2
120...	0.7	3.2	20.6	96.8	21.3	2
150...	0.7	3.5	19.1	96.5	19.8	2
180...	1.9	10.6	16.3	89.4	18.2	2
210...	2.6	16.4	13.3	83.6	15.9	2
240...	4.3	30.3	9.8	69.7	14.1	2
270...	4.4	37.8	7.3	62.2	11.7	2
300...	5.8	52.3	5.3	47.7	11.1	2
330...	4.6	45.9	5.4	54.1	10.0	2
360...	9.2	55.8	7.3	44.2	16.5	2
390...	7.2	51.6	6.8	48.4	14.0	2
420...	11.2	66.3	5.7	33.7	16.9	2
450...	9.3	61.0	6.0	39.0	15.3	2
480...	6.7	55.7	5.3	44.3	12.0	2
510...	8.1	64.7	4.4	35.3	12.5	2
540...	5.8	60.9	3.7	39.1	9.5	2
570...	8.6	66.7	4.3	33.3	12.9	2
600...	6.9	55.1	5.6	44.9	12.5	2
630...	5.9	52.5	5.3	47.5	11.2	2
660...	7.5	61.9	4.6	38.1	12.1	2
690...	8.4	67.8	4.0	32.2	12.4	2
720...	8.2	66.5	4.1	33.5	12.3	2
750...	11.3	66.5	5.7	33.5	17.0	2
780...	11.1	69.9	4.8	30.1	15.9	2
810...	10.5	70.1	4.5	29.9	15.0	2
840...	11.6	74.9	3.9	25.1	15.5	2
870...	11.6	75.2	3.8	24.8	15.4	2
900...	15.2	82.3	3.3	17.7	18.5	2
930...	12.0	76.7	3.6	23.3	15.6	2
960...	11.4	73.1	4.2	26.9	15.6	2
990...	8.1	70.2	3.5	29.8	11.6	2
1020...	9.2	73.6	3.3	26.4	12.5	2
1050...	8.0	68.4	3.7	31.6	11.7	2
1080...	12.2	77.9	3.5	22.1	15.7	2
1110...	10.1	75.2	3.3	24.8	13.4	2
1140...	14.3	81.9	3.2	18.1	17.5	2
1170...	11.4	76.3	3.6	23.7	15.0	2
1200...	11.1	77.6	3.2	22.4	14.3	2
1230...	13.3	80.9	3.1	19.1	16.4	2
1260...	10.6	70.3	4.5	29.7	15.1	2
1290...	12.0	74.1	4.2	25.9	16.2	2
1320...	9.2	71.8	3.6	28.2	12.8	2
1350...	10.1	75.9	3.2	24.1	13.3	2
1380...	9.8	75.7	3.2	24.3	13.0	2
1410...	9.8	73.8	3.5	26.2	13.3	2

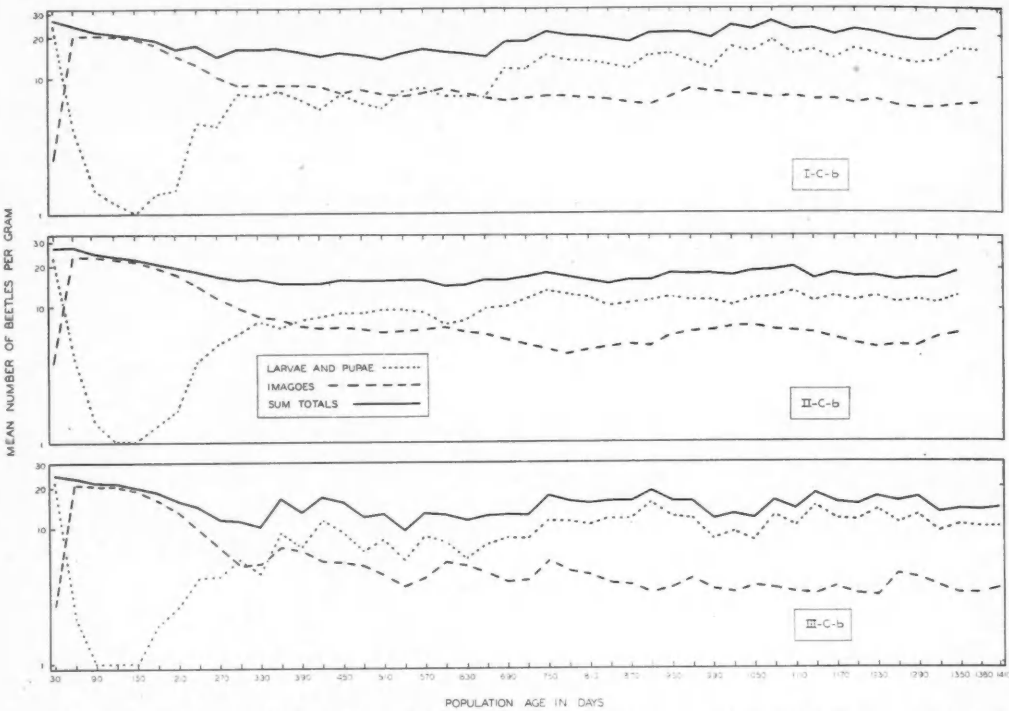

FIG. 1. Census history of I-C-b, II-C-b, and III-C-b populations (*Tribolium confusum*). Mean number of beetles per gram as a logarithmic ordinate is plotted against age in days as the abscissa. Shown are larval-pupal, imaginal, and total population curves (see box).

undoubtedly reflects merely a small-sample effect—it was possible to run only two replicates in all the 80 gram cultures because of their great total size.

Although the pattern is similar between series, there is a tendency for mean total density to be inversely proportional to volume. This will be discussed later when statistical comparisons with *T. castaneum* and the "sterile" populations are introduced. Suffice it to say at this point that the mean total number per gram for Series I is 19.25, while for Series II and III these means are 17.36 and 14.94, respectively (see Table 10). The mean differences in relation to their respective probable errors are all highly significant.

When Figure I is examined with attention focussed on the first 300 days of growth, it is evident that there is exhibited by the larval-pupal and imaginal curves a characteristic "pre-equilibrium period" for all three volumes through which the populations pass before stabilization takes place. During this interval the total population declines somewhat but remains quite stable relative to its component curves. At the first census (30 days) the larval population is large, of course, because there has not been time to produce the first generation of imagoes. Only those imagoes introduced when the cultures were started and still alive are present at this count. By the second census (60 days) many imagoes have emerged and these uniformly young beetles constitute the bulk of the populations: Table 2 lists the number of larvae-pupae and imagoes to be 4.1 and 20.5, respectively, or 17 and 83%. A glance at Tables 3 and 4 shows that the figures are comparable for II-C-b and III-C-b. The number of adult Tribolium remains high during the next 90 days (i.e., to about day-150). These saturate their environment to a large extent and keep down the larval density probably through egg cannibalism, through crowding, and perhaps through other agencies. As these imagoes get older, their death-rate rises and they are reduced in actual numbers as well as in terms of percentages. This is clearly seen in Figure 1. There, the imago populations of all three series begin to decline after day-150 —a decline accompanied by a parallel increase of larvae. This sequence of events is perhaps somewhat oversimplified, but it will be extended shortly. From approximately day-300 to day-660 the larvae-pupae and imagoes are present in closely similar densities. This is more evident in I and II than in III. Thereafter, the larval-pupal curves rise above those for the adults and both remain essentially stabilized for the two year period remaining.

Finally, it is important for the reader to realize that, although the curves we have been discussing are based on averages, they do have validity as descriptions of events within *individual* populations. This

is suggested, of course, by the similarity in pattern between the I, II, and III series. However, more direct evidence was accumulated by graphing single populations one-by-one and then observing that this assemblage of curves conforms closely with the means depicted in Figure 1. As a study of population variability, it would be interesting to publish these figures; but owing to space limitations, this is impracticable although something of the sort may appear at a later date.

TABLE 5. Larvae and pupae, imagoes, and sum totals for **I-C-c** over 1380 days of observation. Data are expressed as mean percentage of larvae and pupae and imagoes per 30-day census period and as mean number of individuals per gram of medium.

Age (days)	Larvae and Pupae		Imagoes		Sum M/gm.	n
	M/gm.	Per cent	M/gm.	Per cent		
30...	17.1	77.5	5.0	22.5	22.1	20
60...	9.3	36.0	16.6	64.0	25.9	20
90...	12.4	42.4	16.9	57.6	29.3	20
120...	12.3	43.4	16.1	56.6	28.4	20
150...	9.9	41.1	14.3	58.9	24.2	20
180...	6.8	36.2	12.1	63.8	18.9	20
210...	4.6	37.0	7.8	63.0	12.4	20
240...	7.5	59.8	5.1	40.2	12.6	20
270...	4.5	66.4	2.3	33.6	6.8	20
300...	6.2	79.8	1.6	20.2	7.8	19
330...	10.7	80.1	2.7	19.9	13.4	18
360...	6.5	66.2	3.3	33.8	9.8	18
390...	8.5	70.4	3.6	29.6	12.1	16
420...	7.9	67.8	3.8	32.2	11.7	16
450...	9.4	71.8	3.7	28.2	13.1	16
480...	7.5	69.2	3.4	30.8	10.9	15
510...	6.8	71.1	2.8	28.9	9.6	15
540...	7.0	68.3	3.2	31.7	10.2	14
570...	7.8	70.3	3.3	29.7	11.1	13
600...	6.9	69.9	3.0	30.1	9.9	13
630...	9.2	76.0	2.9	24.0	12.1	13
660...	7.5	73.1	2.8	26.9	10.3	13
690...	10.1	80.0	2.5	20.0	12.6	13
720...	10.1	77.2	3.0	22.8	13.1	13
750...	11.6	79.5	3.0	20.5	14.6	13
780...	11.0	79.4	2.9	20.6	13.9	13
810...	11.4	79.3	3.0	20.7	14.4	13
840...	10.5	78.6	2.9	21.4	13.4	13
870...	6.7	73.8	2.4	26.2	9.1	13
900...	8.0	79.6	2.1	20.4	10.1	13
930...	10.6	82.7	2.2	17.3	12.8	13
960...	10.6	78.4	2.9	21.6	13.5	13
990...	12.4	82.6	2.6	17.4	15.0	13
1020...	10.8	78.3	3.0	21.7	13.8	13
1050...	9.8	78.0	2.7	22.0	12.5	13
1080...	10.9	81.0	2.6	19.0	13.5	13
1110...	8.3	77.6	2.4	22.4	10.7	13
1140...	8.9	80.7	2.1	19.3	11.0	13
1170...	9.2	76.4	2.8	23.6	12.0	13
1200...	8.2	77.2	2.4	22.8	10.6	13
1230...	7.4	75.9	2.3	24.1	9.7	13
1260...	7.4	76.0	2.3	24.0	9.7	13
1290...	8.0	76.1	2.5	23.9	10.5	13
1320...	7.6	73.8	2.7	26.2	10.3	12
1350...	8.1	74.0	2.8	26.0	10.9	12
1380...	9.0	78.6	2.5	21.4	11.5	12

TRIBOLIUM CASTANEUM CONTROLS (I-C-c, II-C-c, III-C-c)

The data for control populations of *T. castaneum*

TABLE 6. Larvae and pupae, imagoes, and sum totals for **II-C-c** over 1380 days of observation. Data are expressed as mean percentage of larvae and pupae and imagoes per 30-day census period and as mean number of individuals per gram of medium.

Age (days)	Larvae and Pupae		Imagoes		Sum M/gm.	n
	M/gm.	Per cent	M/gm.	Per cent		
30...	13.0	55.5	10.4	44.5	23.4	18
60...	9.1	32.7	18.6	67.3	27.7	18
90...	11.4	38.2	18.6	61.8	30.0	18
120...	9.2	35.4	16.9	64.6	26.1	18
150...	8.2	38.5	13.2	61.5	21.4	18
180...	6.9	43.0	9.1	57.0	16.0	18
210...	3.2	42.6	4.4	57.4	7.6	18
240...	8.1	75.3	2.7	24.7	10.8	18
270...	5.3	76.8	1.6	23.2	6.9	18
300...	6.2	82.4	1.4	17.6	7.6	18
330...	7.7	82.2	1.7	17.8	9.4	18
360...	8.4	79.5	2.2	20.5	10.6	18
390...	8.6	78.9	2.3	21.1	10.9	18
420...	8.1	80.6	1.9	19.4	10.0	18
450...	8.6	81.6	1.9	18.4	10.5	18
480...	7.0	79.8	1.8	20.2	8.8	18
510...	7.0	80.7	1.7	19.3	8.7	18
540...	7.2	79.0	1.9	21.0	9.1	18
570...	6.7	77.9	1.9	22.1	8.6	18
600...	7.1	80.3	1.8	19.7	8.9	18
630...	6.9	81.0	1.6	19.0	8.5	18
660...	5.6	78.1	1.5	21.9	7.1	18
690...	6.9	84.0	1.3	16.0	8.2	18
720...	6.6	83.1	1.3	16.9	7.9	18
750...	7.7	83.9	1.5	16.1	9.2	18
780...	7.9	83.4	1.6	16.6	9.5	18
810...	7.1	82.6	1.5	17.4	8.6	18
840...	5.7	79.4	1.5	20.6	7.2	18
870...	6.2	77.9	1.8	22.1	8.0	18
900...	7.9	81.8	1.8	18.2	9.7	18
930...	9.1	80.7	2.1	19.3	11.2	18
960...	8.8	80.7	2.1	19.3	10.9	18
990...	7.5	81.4	1.7	18.6	9.2	18
1020...	8.2	82.8	1.7	17.2	9.9	18
1050...	7.6	82.3	1.6	17.7	9.2	18
1080...	7.3	82.5	1.6	17.5	8.9	18
1110...	6.7	82.0	1.5	18.0	8.2	18
1140...	6.6	81.8	1.5	18.2	8.1	18
1170...	7.9	82.2	1.7	17.8	9.6	18
1200...	8.3	81.9	1.8	18.1	10.1	18
1230...	8.4	79.6	2.2	20.4	10.6	18
1260...	8.4	78.9	2.2	21.1	10.6	18
1290...	8.8	80.2	2.2	19.8	11.0	18
1320...	9.0	81.1	2.1	18.9	11.1	18
1350...	8.1	80.7	2.0	19.3	10.1	18
1380...	9.1	83.1	1.8	16.9	10.9	18

grown in the three volumes are tabulated in Tables 5, 6, and 7 and graphed in Figure 2, using precisely the same methods of representation as those employed for *T. confusum.*

There is one difference between *T. castaneum* and *T. confusum* in terms of population survival that merits comment. As just reported, no cultures of *T. confusum* became extinct over the entire four-year period. This is equally true for the II and III series of *T. castaneum.* For the eight-gram series (I), however, there were the following eight exceptions out of twenty: one population became extinct at 300 days; one at 330 days; two at 390 days; one at 480 days; one at 540 days; and one at 1320 days. There can be no reasonable doubt but that the failure of these cultures was caused by an added mortality increment resulting from parasitic infection. This merely requires mention here because it will receive further attention shortly.

TABLE 7. Larvae and pupae, imagoes, and sum totals for **III-C-c** over 1410 days of observation. Data are expressed as mean percentage of larvae and pupae and imagoes per 30-day census period and as mean number of individuals per gram of medium.

Age (days)	Larvae and Pupae		Imagoes		Sum M/gm.	n
	M/gm.	Per cent	M/gm.	Per cent		
30...	14.9	63.3	8.6	36.7	23.5	2
60...	7.9	30.4	18.1	69.6	26.0	2
90...	12.9	42.3	17.6	57.7	30.5	2
120...	14.3	46.2	16.7	53.8	31.0	2
150...	12.6	45.5	15.1	54.5	27.7	2
180...	8.1	41.3	11.6	58.7	19.7	2
210...	6.7	48.2	7.2	51.8	13.9	2
240...	11.5	76.6	3.5	23.4	15.0	2
270...	6.1	74.4	2.1	25.6	8.2	2
300...	12.2	91.4	1.2	8.6	13.4	2
330...	12.1	83.7	2.3	16.3	14.4	2
360...	16.6	87.2	2.4	12.8	19.0	2
390...	12.0	80.9	2.8	19.1	14.8	2
420...	18.1	87.9	2.5	12.1	20.6	2
450...	14.8	84.2	2.8	15.8	17.6	2
480...	10.4	79.9	2.6	20.1	13.0	2
510...	16.9	87.4	2.4	12.6	19.3	2
540...	10.6	80.8	2.5	19.2	13.1	2
570...	12.4	84.4	2.3	15.6	14.7	2
600...	12.4	83.7	2.4	16.3	14.8	2
630...	9.6	81.7	2.2	18.3	11.8	2
660...	10.6	81.0	2.5	19.0	13.1	2
690...	11.6	83.6	2.3	16.4	13.9	2
720...	11.2	82.0	2.5	18.0	13.7	2
750...	10.0	80.7	2.4	19.3	12.4	2
780...	12.0	79.7	3.1	20.3	15.1	2
810...	14.6	79.1	3.9	20.9	18.5	2
840...	9.9	70.0	4.3	30.0	14.2	2
870...	9.4	68.0	4.4	32.0	13.8	2
900...	6.6	59.1	4.6	40.9	11.2	2
930...	7.2	60.7	4.7	39.3	11.9	2
960...	6.9	57.4	5.1	42.6	12.0	2
990...	3.7	42.9	5.0	57.1	8.7	2
1020...	9.0	66.7	4.5	33.3	13.5	2
1050...	10.4	69.6	4.5	30.4	14.9	2
1080...	12.6	77.1	3.7	22.9	16.3	2
1110...	9.0	75.8	2.9	24.2	11.9	2
1140...	7.9	79.0	2.1	21.0	10.0	2
1170...	7.4	82.4	1.6	17.6	9.0	2
1200...	3.5	81.6	0.8	18.4	4.3	2
1230...	6.5	88.8	0.8	11.2	7.3	2
1260...	11.2	79.6	2.9	20.4	14.1	2
1290...	9.1	63.5	5.2	36.5	14.3	2
1320...	9.0	65.7	4.7	34.3	13.7	2
1350...	9.2	66.0	4.7	34.0	13.9	2
1380...	10.3	69.4	4.5	30.6	14.8	2
1410...	10.1	71.3	4.1	28.7	14.2	2

Figure 2 makes a point similar to that made by Figure 1, namely: that volume does not affect the pattern of the curves. Under the conditions of this study, populations of *T. castaneum* describe a definite pattern of growth. This pattern is clearly similar for all three series, both in respect of performance by individual populations as well as for averages. The III-C-c curves, based on two replicates, are, again, more erratic than those of I-C-c and II-C-c. There are also relations between mean total density and volume. Over the entire period of observation these means are as follows: I, 13.30, II, 11.23, and III, 15.8 (Table 10). The relation between I and II is in the same direction as that reported for *T. confusum.* There is an exception in that, for *T. castaneum,* the 80 gram volumes (III) produce the largest total populations.

Tribolium castaneum populations also exhibit a pre-equilibrium period as is clearly seen in Figure 2. This period, although diverging in some respects from that shown in Figure 1, is as consistent and characteristic for *T. castaneum* as was the comparable phenomenon just described for *T. confusum.* In both cases, the duration of the period is about the same (approximately 300-330 days) and there are some similarities between the imago curves. There are real differences as well, and a brief recounting of these is appropriate. In the first place, the total population size for *T. castaneum* for all series rises to a maximum during the 90-120 day interval and then falls to assume relative stability from about day-330 on. The imago curves attain their maxima at day-60 but thereafter drop sharply until day-300 when they are lowest. At this time there are only 1.6, 1.4, and 1.2 adults per gram for I, II, and III, respectively. Analogous figures at the same census for *T. confusum* are 8.8, 9.6, and 5.3. The number of imagoes rises somewhat thereafter and remains quite stable over the three remaining years with the exception of a curious drop in III-C-c most pronounced at day-1200. The larval-pupal curves of Figure 2 do not decline so much as those graphed in Figure 1, and their eventual stabilization is at a higher actual, and percentage, level.

Probably the two major differences in terms of growth pattern between the two species when viewed over the entire period of observation lie in the facts (a) that *T. castaneum* maintains itself with a smaller

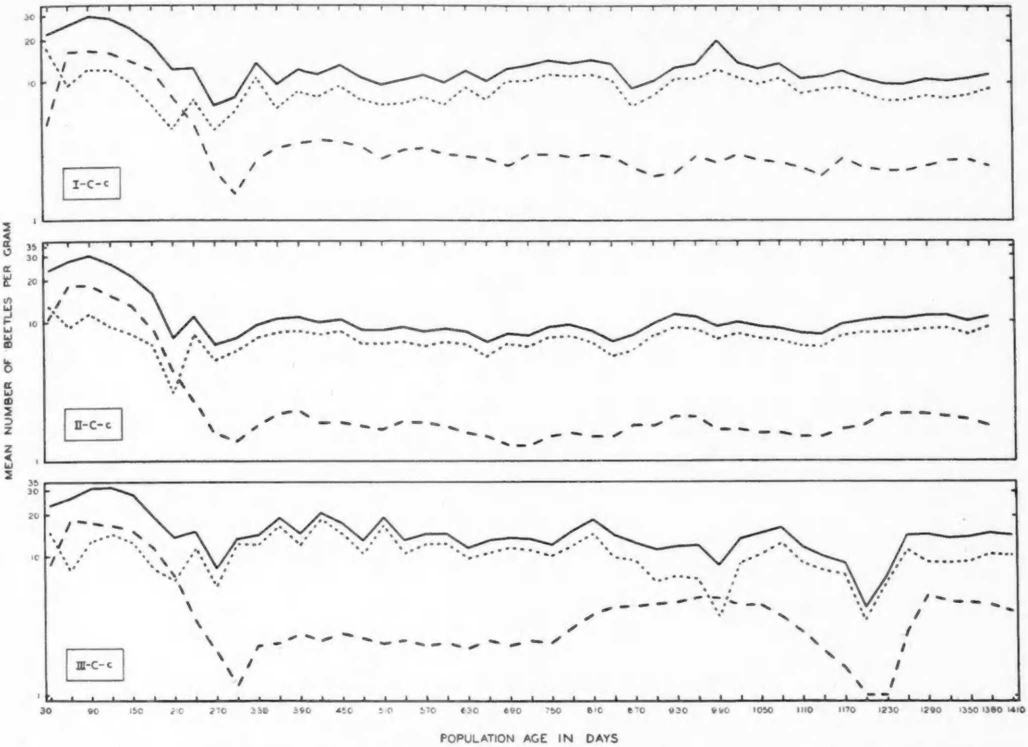

FIG. 2. Census history of I-C-c, II-C-c, and III-C-c populations (*Tribolium castaneum*). Mean number of beetles per gram as a logarithmic ordinate is plotted against age in days as the abscissa. Shown are larval-pupal, imaginal, and total population curves (see box).

number of imagoes, both absolute and relative, and (b) that a depression in total numbers characteristically is seen at day-270 or day-300 which is not displayed by *T. confusum*.

TRIBOLIUM CONFUSUM AND T. CASTANEUM STERILE CONTROLS (I-C-B-S AND I-C-C-S)

In the section dealing with experimental design, and in the discussion of control cultures, the point has been made that both species of Tribolium are infected with a coccidian parasite, Adelina. Also, the inference has been advanced that this infection is related to the population behavior of the beetles and therefore must be considered in an interpretation of the findings. Chapman (1933) and Park, Gregg, and Lutherman (1941) concluded that Adelina infection could alter the course of growth and density of *T. confusum* populations. This, plus the finding of dead larvae and pupae in the siftings when censuses were taken, suggested that the phenomenon should be explored experimentally, thus leading to the establishment of the sterile control and experimental series reported upon in this paper.

Before discussing the actual data, however, it is in order to briefly review certain matters pertaining to this parasite. According to Wenyon (1926) the genus Adelina was founded by Hesse in 1911 to describe an organism parasitic within the oligochaete worm *Slavinia appendiculata*. In 1922 Riley & Krogh discussed a "new species" of coccidian that abundantly infected Tribolium but they did not identify it. In 1923 White mentioned that the fat bodies of both *T. confusum* and *T. castaneum* are invaded by a neosporidian parasite with the usual consequence that the larvae become "sick," distended, partially immobilized, and frequently die. He further noted that pupae and imagoes may also die from infection. White observed that mortality did not appear to any degree during the first month of a population's life-history but that "after a few months" deaths owing to this cause were plentiful. Chapman (1933) and Park (1934; on the basis of studies carried out with *T. confusum* in collaboration with Professor Clay G Huff) independently concluded that this parasite belonged to the genus Adelina. Bhatia (1937) worked with Adelina inhabiting *T. ferrugineum* (= *T. castaneum*) and described the species as *Adelina tribolii*. He also reported some data on its life-cycle, infectivity, and cellular morphology. Yarwood (1937) discusses *A. cryptocerci* whose host is the roach *Cryptocercus punctulatus*. Although her paper is not concerned with flour beetles, it does afford the best general account of the life-cycle of the genus and is useful for this reason. To date, it has not

been critically determined, either by cytological evidence or cross-infection studies, whether *T. confusum* and *T. castaneum* are infected by the same or different species of Adelina. It is a reasonable working presumption that the parasite is taxonomically the same for both hosts. Studies designed to clarify the matter are now under way in this laboratory.

As well as it is understood, the life-cycle of Adelina in Tribolium follows this course. Infection is brought about when the larvae and imagoes ingest mature oöcysts. The oöcysts are taken into the gut as the beetles feed on flour containing them and/or as they feed on living or dead larvae, pupae, and imagoes that are themselves infected. In the mesenteron the oöcysts rupture and liberate motile sporozoites. These penetrate the epithelium passing through it to the haemocoels. The sporozoites invade the host cells, including those of the fat body, and undergo asexual reproduction or schizogony by which process merozoites are produced. These also are motile and further attack the tissues. Apparently schizogony may be repeated a number of times. Eventually sexual reproduction (gametogony) is initiated and gametoblasts differentiate into male and female sex cells. A zygote, formed upon fertilization, starts sporogony—the entire process occurring within a relatively heavy cyst wall. A number of sporoblasts differentiate within each cyst, and these later divide within themselves to form coiled, encased sporozoites. The end-result of the life-cycle is the production in several tissues of many mature oöcysts, each surrounded by a membrane and containing sporozoites. As mentioned above, these are the infective stages, but they do not become infective unless they get out of the first host and into another Tribolium. Since the oöcysts are inactive, they cannot escape through their own activity. Presumably they are liberated only when a beetle dies and breaks apart as typically happens in cultures, or, when such a beetle is cannibalized by its fellows. The nature of the pathology leading to host mortality is not understood. It is known that a beetle can harbor many oöcysts and still remain alive.

Adelina may be readily removed from Tribolium by taking advantage of the fact that the eggs of the latter are never internally parasitized. It is only necessary to separate the oöcysts from the egg membrane, allow the larvae to hatch, and then rear a stock in fresh medium sterilized by heat and prevented from becoming re-infected. By washing the eggs in soap solution to which mercuric chloride (1 : 1,000) is added, the oöcysts are either killed or slough off. This is followed by successive washings in sterile water, the eggs are permitted to dry, and then set aside in covered Petri dishes to await hatching. The young larvae are immediately transferred to the medium. Histological examination has shown this to be an effective method of ridding the beetles of the parasite (Park & Burrows, 1942). It is difficult to maintain Tribolium populations free of Adelina for long periods of time. Despite many tedious precautions (e.g., a separate laboratory and incubator, separate instruments and laboratory clothing, more complicated routines involving frequent heat sterilizations, etc.) some of the cultures eventually become infected. Fortunately, as will be seen later, this did not have serious consequences.

All of the populations designated as "sterile" were maintained in the smallest volume of medium (I); a procedure that reduces time and labor because the total counts relative to the other series are smaller. Since, as has already been seen for both species, volumes II and III diverge so little from I, such a limitation of the study seems legitimate as well as expedient.

The basic data for *Tribolium confusum* sterile con-

TABLE 8. Larvae and pupae, imagoes, and sum totals for **I-C-b-S** over 1140 days of observation. Data are expressed as mean percentage of larvae and pupae and imagoes per 30-day census period and as mean number of individuals per gram of medium.

Age (days)	Larvae and Pupae		Imagoes		Sum M/gm.	n
	M/gm.	Per cent	M/gm.	Per cent		
30...	25.0	95.6	1.1	4.4	26.1	20
60...	5.0	17.8	23.2	82.2	28.2	20
90...	1.5	6.1	23.6	93.9	25.1	20
120...	2.1	8.3	22.9	91.7	25.0	20
150...	1.2	5.1	21.7	94.9	22.9	20
180...	2.2	10.0	20.0	90.0	22.2	20
210...	2.0	10.6	16.7	89.4	18.7	20
240...	3.6	20.9	13.8	79.1	17.4	20
270...	3.2	22.9	10.8	77.1	14.0	20
300...	4.9	34.3	9.4	65.7	14.3	20
330...	4.8	33.3	9.6	66.7	14.4	20
360...	4.2	30.4	9.6	69.6	13.8	20
390...	7.2	42.5	9.7	57.5	16.9	17
420...	4.3	30.6	9.9	69.4	14.2	17
450...	5.4	36.6	9.5	63.4	14.9	17
480...	8.4	47.1	9.5	52.9	17.9	17
510...	10.8	50.4	10.5	49.6	21.3	17
540...	10.7	49.5	11.0	50.5	21.7	17
570...	7.8	34.8	14.5	65.2	22.3	17
600...	3.9	21.9	14.0	78.1	17.9	17
630...	5.4	30.8	12.0	69.2	17.4	17
660...	5.8	33.2	11.5	66.8	17.3	16
690...	7.2	39.6	11.0	60.4	18.2	16
720...	5.7	32.4	12.0	67.6	17.7	16
750...	12.0	47.2	13.3	52.8	25.3	16
780...	6.2	28.6	15.6	71.4	21.8	16
810...	4.4	23.2	14.6	76.8	19.0	16
840...	7.5	36.0	13.3	64.0	20.8	16
870...	5.3	29.3	12.6	70.7	17.9	16
900...	6.7	37.7	11.1	62.3	17.8	16
930...	5.6	34.6	10.5	65.4	16.1	15
960...	10.2	50.2	10.1	49.8	20.3	15
990...	3.5	21.9	12.4	78.1	15.9	15
1020...	6.1	36.9	10.6	63.1	16.7	15
1050...	6.2	37.0	10.5	63.0	16.7	15
1080...	6.0	36.5	10.5	63.5	16.5	15
1110...	6.2	37.2	10.5	62.8	16.7	15
1140...	7.9	42.6	10.7	57.4	18.6	15

trols (I-C-b-S) appear in Table 8 and are graphed as mean number per gram in Figure 3 in which the non-sterile control also is included for purposes of comparison. Figure 4 plots total size only for all series I groups. The *T. castaneum* data appear in Table 9 and Figure 5 and are similarly presented (I-C-c-S). The discussion will be developed by contrasting infected *T. confusum* with sterile *T. confusum* populations to be followed by a like treatment for populations of *T. castaneum*. Comparisons between the two species relative to the presence and absence of Adelina is then attempted.

It is possible to quickly summarize the differences and similarities between I-C-b and I-C-b-S by reference to Tables 2 and 8 and Figures 3 and 4.

In the first place, none of the individual cultures

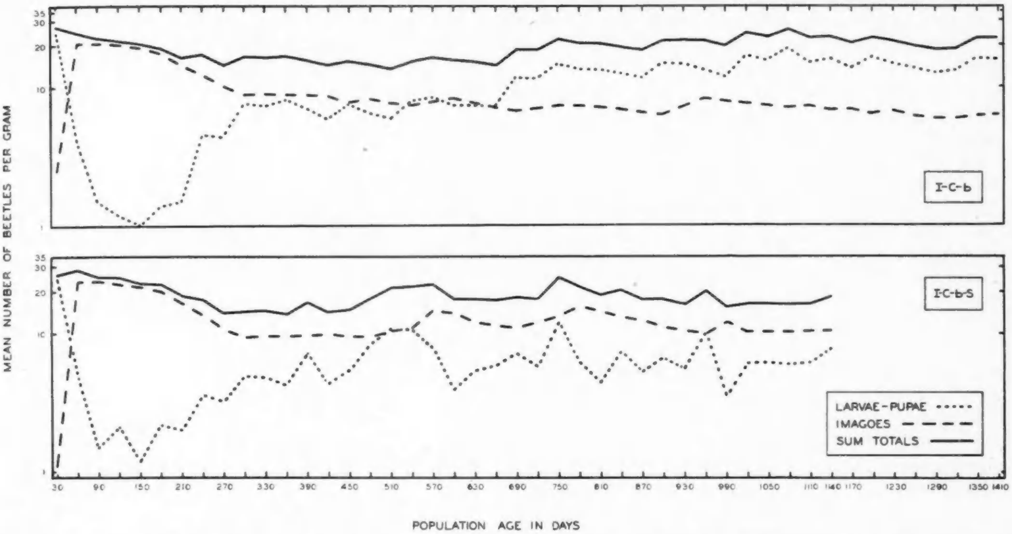

FIG. 3. Census history of *Tribolium confusum* infected controls (I-C-b) compared with *T. confusum* sterile controls (I-C-b-S). Shown are larval-pupal, imaginal and total population curves (see box). Logarithmic ordinate; arithmetical abscissa.

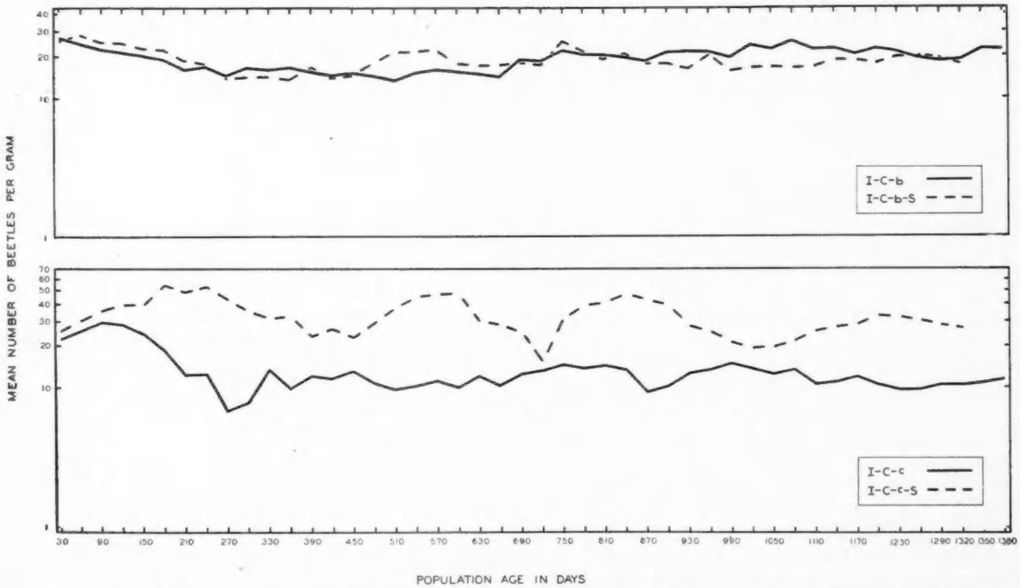

FIG. 4. Census history, in terms of total population size only, of *T. confusum* infected compared with *T. confusum* sterile (I-C-b cf. I-C-b-S) and *T. castaneum* infected compared with *T. castaneum* sterile (I-C-c cf. I-C-c-S). The reduced density of I-C-c-S shown at day-720 is caused by inadvertent low temperature as explained in text. Logarithmic ordinate; arithmetical abscissa.

became extinct over the entire period of observation. The reduction in the *n*-column of Table 8 subsequent to day-360 signifies inadvertent infection, not extinction.

In the second place, it is evident that total population size is unaffected by Adelina. This can be readily seen in Figures 3 and 4 or by comparison of the mean per gram columns of Tables 2 and 8. The divergence between the two curves along the time axis is accounted for by accidents of sampling. When the means for the entire period of observation are computed, they have the values 19.25 and 18.94 for I-C-b and I-C-b-S, respectively (Table 10). The mean difference is 0.31 with P., exceeding 50 per cent.

The third point is that a pre-equilibrium period is passed through by the sterile cultures also. This period is essentially similar to that displayed by the infected populations with the exception that the rise of the larval-pupal curve after day-210 is less pronounced.

The fourth point involves a fundamental difference between the two types of cultures rather than a similarity. The sterile *T. confusum* populations maintain themselves with a significantly greater number of imagoes, and a significantly smaller number of larvae-pupae, than do the infected populations both in terms of means per gram and percentages. This is especially evident after day-240. It leads to the speculation that something more than half a year is required before infection of *T. confusum* by Adelina, at least under these conditions of husbandry, reaches a degree sufficient to cause the infected cultures to deviate consistently from the steriles in terms of their composition by stages. The most probable interpretation of this deviation between the I-C-b and I-C-b-S series is, that in the absence of Adelina, there are fewer deaths in the late larval and pupal periods with the consequence that more imagoes emerge. It is interesting to note that the total size of the sterile populations, despite the fact that they contain more reproducers (imagoes), does not increase and exceed that of infected cultures (Fig. 4). As has been shown, this clearly does not happen. In explanation of this, one hypothesis is that some sort of balance exists between food supply and mean total population beyond the upper limit of which the cultures do not go. Another hypothesis is that the total *net*-reproduction of the sterile groups actually is not higher than that of the infected even though more adults are present. This heightened imago density could reduce the average rate of fecundity per female per unit of time, or increase the rate of egg cannibalism, or both. These hypotheses, and others that could be advanced, lend themselves to experimental analysis and verification—an analysis that should be forthcoming at a later date as the entire program on interspecies competition matures.

Up to this point, an impression of essential similarity between control cultures may have been established in the mind of the reader. Such similarities prevail in several directions: in terms of volume of medium, composition by stages, pattern of growth with time, equilibria, presence or absence of parasitization, and, to a considerable extent, even between species. This is not to say that important differences do not exist as well. They do, and certain of them have been described. But probably the general conception is more one of conformity than of divergence. When Adelina is removed from populations of *T. castaneum*, however, this conception is altered considerably. The I-C-c-S cultures, while consistent within themselves as a group of replicates, differ both quantitatively and qualitatively from all other controls. Because this phenomenon is interesting in its own right from the viewpoint of epidemiology, and

TABLE 9. Larvae and pupae, imagoes, and sum totals for **I-C-c-S** over 1140 days of observation. Data are expressed as mean percentage of larvae and pupae and imagoes per 30-day census period and as mean number of individuals per gram of medium.

Age (days)	Larvae and Pupae		Imagoes		Sum M/gm.	*n*
	M/gm.	Per cent	M/gm.	Per cent		
30...	22.2	86.8	3.4	13.2	25.6	20
60...	10.9	36.1	19.3	63.9	30.2	20
90...	15.6	44.3	19.6	55.7	35.2	20
120...	18.7	47.1	21.1	52.9	39.8	20
150...	18.0	45.2	21.8	54.8	39.8	20
180...	32.0	58.9	22.3	41.1	54.3	19
210...	20.8	42.8	27.7	57.2	48.5	18
240...	23.5	46.8	26.8	53.2	50.3	18
270...	18.6	43.4	24.3	56.6	42.9	18
300...	15.1	43.1	20.0	56.9	35.1	18
330...	14.7	46.6	16.9	53.4	31.6	18
360...	17.0	52.2	15.6	47.8	32.6	18
390...	12.5	53.6	10.8	46.4	23.3	18
420...	15.4	57.6	11.3	42.4	26.7	18
450...	11.5	49.9	11.5	50.1	23.0	18
480...	17.6	60.6	11.4	39.4	29.0	18
510...	25.3	66.9	12.6	33.1	37.9	18
540...	26.3	59.2	18.1	40.8	44.4	18
570...	25.8	55.7	20.6	44.3	46.4	18
600...	25.9	54.8	21.3	45.2	47.2	18
630...	12.2	40.5	17.9	59.5	30.1	17
660...	11.9	42.1	16.5	57.9	28.4	17
690...	10.6	41.9	14.7	58.1	25.3	17
720*..	6.0	39.1	9.4	60.9	15.4	17
750...	23.2	72.2	8.9	27.8	32.1	17
780...	22.9	60.1	15.3	39.9	38.2	17
810...	23.3	57.5	17.2	42.5	40.5	17
840...	27.6	58.4	19.6	41.6	47.2	16
870...	22.4	52.8	20.1	47.2	42.5	14
900...	20.2	50.8	19.6	49.2	39.8	13
930...	10.9	39.1	17.0	60.9	27.9	13
960...	11.9	46.5	13.7	53.5	25.6	11
990...	10.5	49.5	10.6	50.5	21.1	11
1020...	10.9	56.0	8.6	44.0	19.5	10
1050...	12.3	62.0	7.5	38.0	19.8	9
1080...	14.3	65.4	7.6	34.6	21.9	9
1110...	15.8	61.1	10.1	38.9	25.9	9
1140...	15.8	57.5	11.6	42.5	27.4	9

* See discussion of this census in text.

because it has an interpretative bearing on the problem of interspecies competition to be reviewed later, it is advisable to discuss the sterile *T. castaneum* controls in some detail, paying particular attention to them in comparison with infected populations of the same species.

From inspection of Figures 4 and 5 and certain of the tables, the following points are to be noted:

(1) None of the I-C-c-S cultures became extinct. As was true for I-C-b-S, some do acquire the parasite and these are then dropped from the computations. This accounts for the reduction in the *n*-column of Table 9; a greater reduction than that evident for *T. confusum*.

(2) In terms of total size, the sterile populations are larger than the infected at every point along the time axis. At the period when the two curves are closest together (720 days) the mean difference between these two points is 15.4 − 13.1 = 2.3.[2] Typically, the curves are much farther apart as is evident in the following tabulation showing differences (I-C-c-S minus I-C-c) arbitrarily selected at intervals of 150 days:

Day 90: 35.2 — 29.3 = 5.9 ± 1.74
Day 240: 50.3 — 12.6 = 37.7 ± 3.95
Day 390: 23.3 — 12.1 = 11.2 ± 1.54
Day 540: 44.4 — 10.2 = 34.2 ± 2.54
Day 690: 25.3 — 12.6 = 12.7 ± 1.82
Day 840: 47.2 — 13.4 = 33.8 ± 2.27
Day 990: 21.1 — 15.0 = 6.1 ± 1.64
Day 1140: 27.4 — 11.0 = 16.4 ± 1.42

These differences are all highly significant in relation to their probable errors.

For the entire period of study the mean range (maximum to minimum) for the steriles is 54.3 to 19.5; for the infected, 29.3 to 9.1. The actual differences between these ranges in terms of numbers per gram are 34.8 and 20.2. For the sterile cultures, the minimum is 36 per cent of the maximum; for the infected, 31% of the maximum.

Over 1140 days of observation for the steriles, and 1380 days of observation for the infected, the mean total population sizes are 33.48 and 13.30, respectively. This difference of 20.18 is highly significant statistically with P.<0.0000. In other words, the removal of infection by Adelina without any other known change in the populations' nutritional potential, physical environment, or husbandry, increases average size by two and a half times! This has significant implications. It suggests, under these experimental conditions of course, that a culture of *T. castaneum* is not limited by lack of food to that lower equilibrium maintained by I-C-c. It suggests that Adelina, when present in sufficient degree, has such potent adverse effects upon the beetles that lower densities result. Further, these effects must be specific for *T. castaneum* only. *T. confusum*, although its composition as to stages is influenced by parasitization, is not influenced so far as total numbers go.

(3) In addition to the fact just noted that the total size of *T. castaneum* sterile cultures is consistently greater than that of the infected cultures, there is also some divergence in the early trend of the two curves, as seen in Figure 4. The infected populations drop rather sharply from day-120 to day-270 —a drop not duplicated by the steriles. Presumably this drop reflects a build-up in infection pressure leading to subsequent mortality. In this connection, it is worth remembering that, although Adelina is present when the parasitized cultures are started, it is not present to any great extent because the few seeding imagoes are reared from *eggs* in clean medium. Thus, some time is required before the parasite gets well established. After some sort of numerical stabilization is reached between host and parasite populations, the curve of total numbers for I-C-c remains fairly level and the percentages of larvae-pupae to imagoes remain quite constant; the former comprising approximately 70 to 80 per cent of the total.

(4) As a preliminary to writing this manuscript, many study-graphs, assembled and plotted in different ways and designed to compare various phenomena, were constructed. Obviously, most of these cannot be reproduced owing to limitations of space and certain of them should not be incorporated into this report because they would obfuscate the major argument. Among these graphs, however, was one plotting mean total size of I-C-b, I-C-b-S, I-C-c, and I-C-c-S cultures. The co-ordinates of this figure were purposely exaggerated to emphasize variability in time within and between each of the four series by using an arithmetical, instead of a logarithmic, ordinate (mean per gram) and by contracting the abscissa (age in days) relative to the ordinate. Under these circumstances, an interesting feature emerges that can be seen in Figures 4 and 5 but that might be overlooked if one was not searching for it, namely: that the sterile *T. castaneum* populations pass through fluctuations of considerable amplitude consisting of

[2] This low figure of 15.4 has considerable physiological and ecological interest in its own right and merits further elaboration. Inadvertently, a failure in electrical power during the 690-720 day interval caused the sterile incubator (only) to drop to room temperature for some two to three weeks. It seems evident (a) that the low population density of *T. castaneum* at the 720 day census is caused by cold, and (b) that this depression does not obtain to any degree, if at all, for *T. confusum* cultures which were in the same chamber. The response was uniformly exhibited by *all* I-C-c-S replicates as the following protocol, comparing the total population size in number of beetles per eight grams of medium, clearly shows:

Replicate Number	Census age (days) 690	720	750
2	175	90	230
3	200	132	274
4	192	103	205
5	198	150	207
6	190	95	233
7	139	92	159
8	224	142	269
10	161	75	221
11	169	107	240
13	183	111	262
14	297	124	217
15	259	243	386
16	240	142	354
17	184	118	204
18	160	103	310
19	277	162	347
20	201	106	246

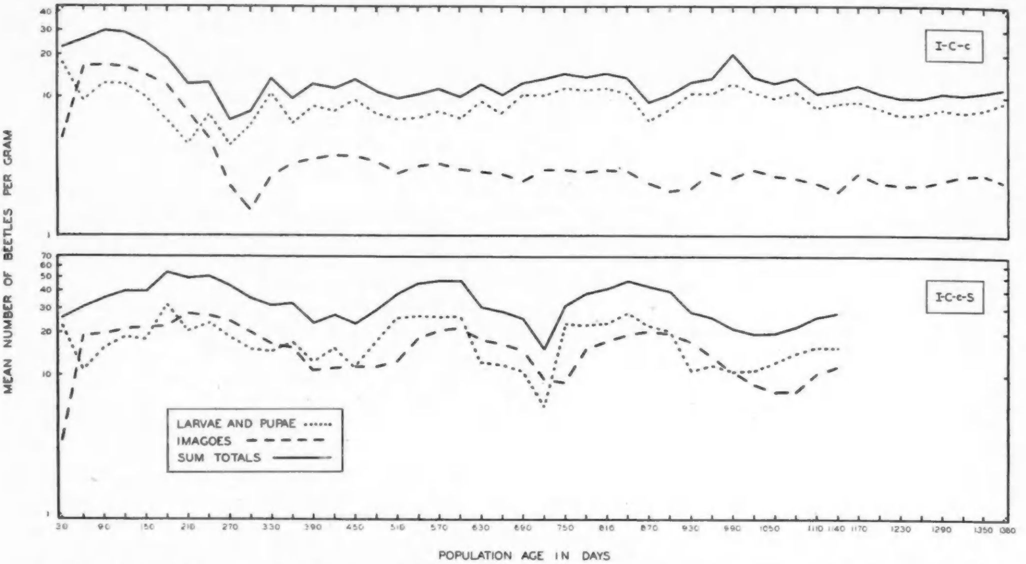

FIG. 5. Census history of *Tribolium castaneum* infected controls (I-C-c) compared with *T. castaneum* sterile controls (I-C-c-S). Shown are larval-pupal, imaginal, and total population curves (see box). Logarithmic ordinate; arithmetical abscissa. Low density of I-C-c-S at day 720 caused by cold (see text).

high peaks and low depressions. These are rather evenly spaced in time and are more characteristic of I-C-c-S than of the other groups. Peaks occur at 180, 600, 840, and 1200 days; and depressions, at 450, 720, and 1020 days.

It is of particular interest to report that these peaks and depressions are not primarily created by averaging the data and therefore do not represent artifacts in the sense that several extreme readings, either high or low, could produce them. Certainly something of this obtains, but, essentially, they are real phenomena exhibited at particular ages, or over several age ranges, by many of the individual populations.

(5) It has been shown for the I-C-b, I-C-b-S, and I-C-c cultures that there exists a pre-equilibrium period of some 300 days' duration during which the imagoes increase rapidly in numbers until they constitute well over half of the total population and then decline until a state of equilibrium, or, better, a state of relative stability, is reached. This varies in detail between the three types of controls. There is no comparable period in the sterile *T. castaneum* cultures as a glance at Figure 5 will show. After the sixtieth day, both larval-pupal and imaginal curves are close together and intercross. Thus, there is as much stability in composition in the early population history as there is later—perhaps even more.

(6) This crossing-over of the imaginal and larval-pupal curves of I-C-c-S characterizes the entire period and is not seen in I-C-c. In other words, the percentage composition of imagoes is higher in the absence of Adelina, an effect also noted for *T. confusum* and one to be anticipated because of the reduction of late larval and pupal mortality. The mean percentage of imagoes for the total period is 48.2 for the steriles and 29.5 for the infected ($P < 0.0000$) (Table 12).

(7) In sum, it seems clear (a) that Adelina strikingly affects *T. castaneum* in terms of total population size while having no such effect on *T. confusum;* (b) that both species of beetles are similarly affected in the sense that the sterile cultures stabilize with a higher proportion of imagoes than do the infected cultures; (c) that removal of the parasite permits *T. castaneum* to exploit its environment in a remarkable way; and (d) that a characteristic pre-equilibrium period is absent in I-C-c-S.

By taking advantage of the misfortune that certain I-C-c-S cultures become infected with Adelina, it is possible to analyze further the relation of infection to total population size.

The data bearing on this were accumulated as follows. There are the sterile populations (I-C-c-S) that never became parasitized. There are populations initially of the same sort that go through a period free of Adelina only later to acquire the disease. There are the regular controls (I-C-c) that were always parasitized. These three groups can be compared with such comparisons made, not relative to a census age fixed for the entire sample, but relative to that time at which infection was first noted. If a certain I-C-c-S culture became parasitized, say, at day-630 and another at day-900, these were dealt with by tabulating, first, the total population counts one-by-one for each culture over 300 days preceding the infection (10 censuses) and, second, the counts for 240 days after the infection had been acquired (8 censuses). In order to have a legitimate control against which these "preinfection" and "infection"

intervals could be tested, other always-sterile cultures were arbitrarily selected for every age represented in the sterile-becoming-infected sample. Mean total population size was computed for this sample; first, for the 300-day period, then, for the 240-day period. Each of these two I-C-c-S groups over the 540 days are represented by seven replicates. In addition, mean total size for seven I-C-c cultures was calculated for the last 240 days—the various census ages again being chosen in the same way. These means along with their probable errors are as follows:

I-C-c-S Cultures:

First interval (300 days)	
(a) Populations not infected	32.44 ± 0.9188
(b) Populations not infected, but to become infected	34.61 ± 1.3702
(c) (a) + (b)	33.53 ± 0.8208
Second interval (240 days)	
(d) Populations not infected (sample (a) above)	26.45 ± 0.8947
(e) Populations infected (sample (b) above)	18.22 ± 0.7487

I-C-c Cultures:

(f) Populations always infected (second interval)	10.75 ± 0.3397

In this table (a) and (b) do not differ significantly from each other ($P = 38.1\%$). The following differences are significant ($P<5\%$): a minus d, b minus e, d minus e, and e minus f.

The most instructive point emerging from the table is, that after those populations originally sterile become parasitized (sample-e) their total size is significantly reduced below that of the cultures remaining sterile (sample-d), the mean difference being 8.23 ± 1.61. The sterile cultures also decline from an average of 32.44 for the first interval to one of 26.45 for the second interval—a decline obviously not induced by Adelina. It is worth noting that the I-C-c controls (sample-f) are considerably lower than is the mean for sample-e. Probably in the latter group there has not been enough time for the infection to attain maximum saturation.

Concluding Statement about Adelina Infection

It is reasonable to conclude that Adelina influences *T. castaneum* populations through the agency of increased mortality directed especially to the immature stages. This conclusion is warranted from knowledge of the parasite and its life-cycle, from the observed census differences between infected and sterile populations, and from the "clinical" appearances of the two sorts of cultures at the time of counting when many dead larvae and pupae are present in the I-C-c replicates but essentially absent in the I-C-c-S. It does not necessarily follow, however, that culture growth is stimulated in the absence of Adelina only through reduction of the specific death-rate. Perhaps fecundity is heightened also; a point not yet analyzed. It should be recalled here that *T. castaneum*, under optimal conditions at least, possesses a reproductive capacity higher than that of *T. confusum*. This may be a factor favoring the demonstrated increase of I-C-c-S cultures.

There are other aspects to this entire matter of infection that are not yet clear. Why is it that *T. castaneum* steriles attain such a higher density than do those of *T. confusum?* Why, when the number of *T. confusum* imagoes increases as it does in the I-C-b-S series, does not total population size also increase? What limits, or, conversely stated, fails to stimulate, *T. confusum* in the absence of infection that works in the opposite direction for *T. castaneum?* Why is it that infection pressure can mount to a degree sufficient to cause certain of the I-C-c controls to become extinct when this never happens in the II and III volumes nor in any of the *T. confusum* populations? Is Adelina more infectious for *T. castaneum* than for *T. confusum* assuming only one species of parasite is incriminated, or, are both beetles equally susceptible with the infection resulting in greater pathology in *T. castaneum?* Are there any immune phenomena operating as part of this host-parasite interaction? Do the findings suggest a longer evolutionary association with better adaptation between *T. confusum* and Adelina than between *T. castaneum* and Adelina?

These are fascinating questions but ones that cannot be answered at this time. It is only possible to present the facts descriptively and postpone more final interpretations pending further study.

Percentage Composition of Control Populations

As an extension of the preceding discussion devoted largely to actual numbers per gram, it is helpful to examine and compare the eight types of control populations in terms of their percentage composition by stages. These percentages have already been reported in Tables 2-9, but the trends are more quickly evident in Figures 6 and 7.

A word about the construction of the two figures is appropriate. The ordinate is a percentage scale ranging from zero to 100 and the abscissa is a time scale reporting age by thirty-day census intervals. Each curve describes a particular type of population and is plotted from points computed as means of all replicates. The distance from the baseline to the curve is the percentage of larvae-pupae while the distance up from the curve to the horizontal line drawn at 100 per cent is the percentage of imagoes. Thus, when the curve is close to the abscissa, the proportion of imagoes is high; and, conversely, as the curve rises, the proportion of imagoes decreases and that of the larvae-pupae increases.

The figures are drawn, in each case, to compare two different control populations. Figure 6 compares I-C-b with I-C-c; II-C-b with II-C-c; III-C-b with III-C-c; and C-b with C-c, the three volumes being averaged. Figure 7, concerned entirely with the eight gram volume (I), compares I-C-b with I-C-b-S; I-C-c with I-C-c-S; and I-C-b-S with I-C-c-S.

In summary of percentage composition, the following points can be advanced:

(1) *Volume of medium.*—The curves of Figure 6 are consistent in pattern for each species, irrespec-

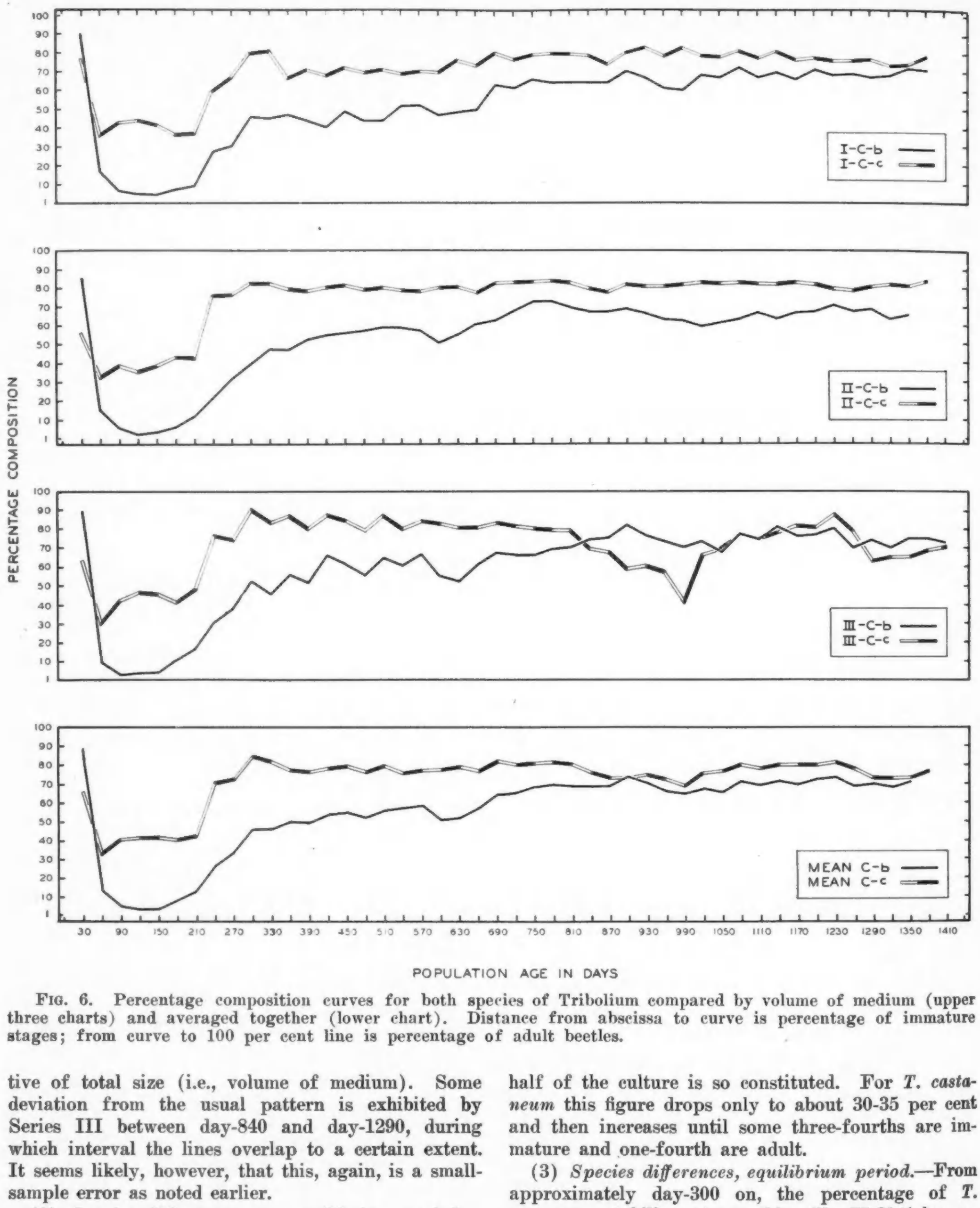

FIG. 6. Percentage composition curves for both species of Tribolium compared by volume of medium (upper three charts) and averaged together (lower chart). Distance from abscissa to curve is percentage of immature stages; from curve to 100 per cent line is percentage of adult beetles.

tive of total size (i.e., volume of medium). Some deviation from the usual pattern is exhibited by Series III between day-840 and day-1290, during which interval the lines overlap to a certain extent. It seems likely, however, that this, again, is a small-sample error as noted earlier.

(2) *Species differences, pre-equilibrium period.*—The percentage curves clearly describe the pre-equilibrium period for populations of both species of beetles and illustrate the species differences that obtain over this first 300 days. The proportion of larvae-pupae for *T. confusum* drops rapidly to a place where they comprise less than five per cent of the total population, then gradually rises until about half of the culture is so constituted. For *T. castaneum* this figure drops only to about 30-35 per cent and then increases until some three-fourths are immature and one-fourth are adult.

(3) *Species differences, equilibrium period.*—From approximately day-300 on, the percentage of *T. castaneum* stabilizes at something like 75-80% larvae-pupae, while *T. confusum* first stabilizes at about 50-60%. The latter curves then rise very slowly until they eventually come quite close to the proportions characteristic for *T. castaneum.*

(4) *Species differences, sterile and infected populations.*—The top graph of Figure 7, comparing I-C-b with I-C-b-S, extends the discussion already

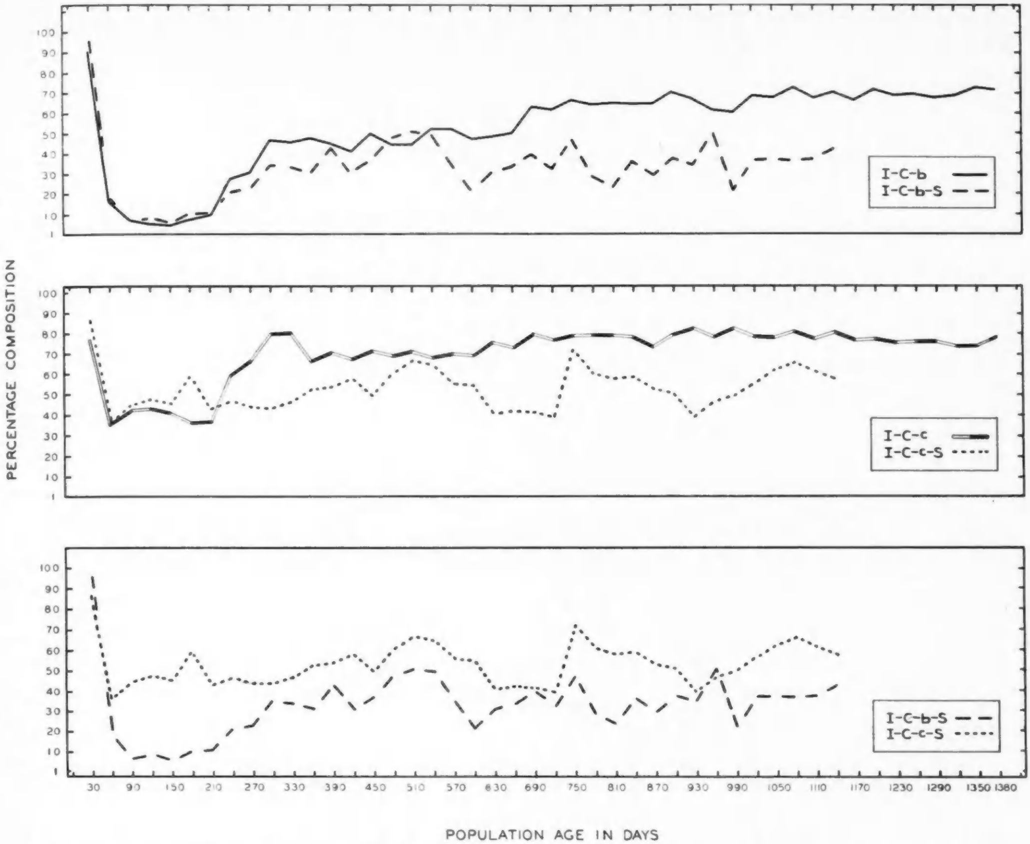

FIG. 7. Percentage composition curves for infected and sterile cultures of *T. confusum* and *T. castaneum* maintained in the eight-gram volume of medium. Respective comparisons indicated within the boxes.

presented based on actual numbers per gram. There is a close degree of confluence between the two curves until day-210, after which the sterile populations are characterized by a larger proportion of imagoes. According to our hypothesis, it requires about this much time for an Adelina infection to become sufficiently established so that mortality reduces the emergence of pupae from larvae, and the eclosion of imagoes from pupae. By day-1140 the adult percentages are 30.0 and 57.4 for infected and sterile, respectively.

In viewing the middle graph (I-C-c and I-C-c-S) it should be remembered that the sterile cultures are much larger both as totals as well as larvae-pupae and imagoes. From day-60 to day-210 the steriles exhibit a slightly lower percentage of imagoes than do the infected. After day-240, as even casual inspection will show, the sterile populations maintain themselves with a significantly higher proportion of imagoes: for example, at day-1140, I-C-c has 19.3% and I-C-c-S, 42.5%.

The bottom graph of Figure 7, contrasting the steriles of both species, suggests (a) that *T. confusum* still maintains a higher percentage of imagoes than does *T. castaneum* even though Adelina is absent, and (b) that the general effect of removing the parasite is to increase the proportion of adult beetles for both species of Tribolium to about the same degree.

CONTROL CULTURES CONSIDERED OVER THE TOTAL PERIOD: A SUMMARY

To afford a final summary, the eight types of single-species populations are now examined when averaged for the entire period of study—a period of nearly four years' duration. The topics considered are: statistics dealing with mean numbers per gram; statistics concerned with percentage composition; and statistics that describe variability.

Mean Number per Gram.—Table 10 lists for each type of control the range, mean, standard deviation, and coefficient of variability for larvae-pupae, imagoes, and sum totals. Table 11 records certain statistical comparisons between selected mean differences in relation to their probable errors. Figure 8 graphs the means for all types of cultures.

Our interest lies in summarizing very briefly four relationships, each considered from the point of view

TABLE 10. Statistics in terms of numbers per gram for total period of study.

Population	Stages	Mean Range		Mean ± P. E.	Standard Deviation	C. V.	n	Days Observed
		Maximum	Minimum					
I-C-b	L + P	18.6	0.96	10.38±0.52	5.25	50.6	46	1380
	I	20.6	5.9	8.87±0.41	4.15	46.8	46	1380
	Total	25.6	13.6	19.25±0.33	3.32	17.2	46	1380
I-C-b-S	L + P	12.0	1.2	6.21±0.43	3.98	64.1	38	1140
	I	23.6	9.4	12.73±0.53	4.82	37.9	38	1140
	Total	28.2	14.0	18.94±0.40	3.67	19.4	38	1140
II-C-b	L + P	12.8	0.6	8.97±0.40	3.94	43.9	45	1350
	I	23.5	4.4	8.39±0.53	5.31	63.3	45	1350
	Total	27.7	14.1	17.36±0.31	3.09	17.8	45	1350
III-C-b	L + P	15.2	0.6	8.66±0.40	4.09	47.2	47	1410
	I	21.1	3.2	6.28±0.49	4.99	79.5	47	1410
	Total	23.3	9.5	14.94±0.32	3.28	21.9	47	1410
I-C-c	L + P	12.4	4.4	8.98±0.23	2.27	25.3	46	1380
	I	16.9	1.6	4.32±0.39	3.95	91.4	46	1380
	Total	29.3	9.1	13.30±0.48	4.85	36.5	46	1380
I-C-c-S	L + P	32.0	6.0	17.63±0.66	6.00	34.0	38	1140
	I	27.7	7.5	15.85±0.62	5.63	35.5	38	1140
	Total	54.3	19.5	33.48±0.32	9.79	29.2	38	1140
II-C-c	L + P	11.4	3.2	7.72±0.15	1.53	19.8	46	1380
	I	18.6	1.3	3.51±0.44	4.48	127.6	46	1380
	Total	30.0	7.1	11.23±0.53	5.37	47.8	46	1380
III-C-c	L + P	18.1	3.5	10.48±0.31	3.13	29.9	47	1410
	I	18.1	0.8	4.70±0.41	4.17	88.7	47	1410
	Total	30.5	7.3	15.18±0.53	5.39	35.5	47	1410

of the total population, the number of imagoes, and the number of larvae-pupae. These relationships are:[3]

(1) Between volumes, within species (b in I, II, III; c in I, II, III)

(2) Between species, within volumes (b cf. c in I; b cf. c in II; b cf. c in III)

(3) Between parasitized and non-parasitized, within species and within volume (I-C-b cf. I-C-b-S; I-C-c cf. I-C-c-S)

(4) Between non-parasitized species, within volume (I-C-b-S cf. I-C-c-S)

Between Volumes, within Species.—It is clear from the tables and Figure 8 that the total population size of *T. confusum*, expressed as density of organisms per gram of medium, decreases significantly with increase of volume. Similar relations hold for larvae-pupae and adults, but only the difference between I-imagoes and III-imagoes is clearly significant. Because the trend is consistent, however, it is a reasonable conjecture that such an association of density with size of environment does exist.

The situation for *T. castaneum*, on the other hand, is not the same; namely, III>I>II with only the difference between III and II being decidedly significant (P values for III cf. I and I cf. II are borderline). While there is no indication of a trend between volumes so far as imagoes are concerned, it is obvious that the III populations maintain themselves with a greater number of immature stages and that I exceeds II in this respect.

One is then left with the conception (a) that volume of medium can be significantly correlated with density, and (b) that, while this correlation is quite consistent for *T. confusum* in a negative direction, it is not so clearcut for *T. castaneum*. An important point has been made earlier that volume, even though it affects density, does not appreciably alter the pattern or course of the populations in time.[4]

Between Species, within Volumes.—In terms of total population size, *T. confusum* in the 8 and 40 gram environments maintains itself at a significantly higher level than does *T. castaneum* with no appreciable difference displayed for the 80 gram environments. In other words, I-b>I-c by about 30%, II-b>II-c by about 35%, and III-b = III-c. Similar relations hold for the immature and adult stages of I and II considered independently although the number of *T. confusum* larvae-pupae in the smallest volumes does not differ significantly from that of *T.*

[3] In the statistical sense, two "interactions" are encompassed by this treatment: the interaction between species and volume, and that between species and parasitism.

[4] It is recognized that even though 47 entries, representing 47 consecutive censuses, comprise the III-C-b and III-C-c samples, actually these are based on only two replicates. Thus, their means do not have as much reliability as do those of the I and II series. This is unfortunate but, as pointed out earlier, quite unavoidable. We still place considerable general confidence in the samples, however, because they display a close similarity in pattern of growth to that shown by the two smaller volumes based on larger numbers. (Fig. 1, 2.)

TABLE 11. Statistical analysis of selected mean differences reported in Table 10 (by mean difference ÷ its probable error).

The Comparison	Stage	Mean difference	Largest member of pair	Probability
I-C-b and I-C-b-S	L and P	4.17	I-C-b	<0.0000
	I	3.86	I-C-b-S	<0.0000
	T	0.31	I-C-b	>0.5
I-C-b and II-C-b	L and P	1.41	I-C-b	0.1567
	I	0.48	I-C-b	>0.5
	T	1.89	I-C-b	0.0046
I-C-b and III-C-b	L and P	1.72	I-C-b	0.0795
	I	2.59	I-C-b	0.0070
	T	4.31	I-C-b	<0.0000
II-C-b and III-C-b	L and P	0.31	II-C-b	>0.5
	I	2.11	II-C-b	0.0505
	T	2.42	II-C-b	<0.0000
I-C-c and I-C-c-S	L and P	8.65	I-C-c-S	<0.0000
	I	11.53	I-C-c-S	<0.0000
	T	20.18	I-C-c-S	<0.0000
I C-c and II-C-c	L and P	1.26	I-C-c	0.0019
	I	0.81	I-C-c	0.3450
	T	2.07	I-C-c	0.0505
I-C-c and III-C-c	L and P	1.50	III-C-c	0.0085
	I	0.38	III-C-c	>0.5
	T	1.88	III-C-c	0.0795
II-C-c and III-C-c	L and P	2.76	III-C-c	<0.0000
	I	1.19	III-C-c	0.1773
	T	3.95	III-C-c	<0.0000
I-C-b and I-C-c	L and P	1.40	I-C-b	0.0918
	I	4.55	I-C-b	<0.0000
	T	5.95	I-C-b	<0.0000
I-C-b-S and I-C-c-S	L and P	11.42	I-C-c-S	<0.0000
	I	3.12	I-C-c-S	0.0085
	T	14.54	I-C-c-S	<0.0000
II-C-b and II-C-c	L and P	1.25	II-C-b	0.0430
	I	4.88	II-C-b	<0.0000
	T	6.13	II-C-b	<0.0000
III-C-b and III-C-c	L and P	1.82	III-C-c	0.0152
	I	1.58	III-C-b	0.0918
	T	0.24	III-C-c	>0.5

castaneum ($P = 9\%$). Within series-III the only statistically significant difference is that for the immature stages—the mean number being greater for *T. castaneum* than for *T. confusum* ($P = 1.5\%$).

Between Parasitized and Non-parasitized, within Species, within Volume.—This relation has already been established and requires only brief summary here. The essential points are as follows:

(1) *T. confusum*-infected and *T. confusum*-sterile cultures maintain populations of equivalent total size. The latter group is characterized by more imagoes and fewer larvae-pupae. Both differences are highly significant ($P<0.0000$ in each instance). The matter of the higher imago densities in populations free of Adelina was discussed earlier.

(2) Non-infected *T. castaneum* cultures are decidedly larger than the infected over the entire period of observation. The mean differences are:

for total size,	$33.48 - 13.30 = 20.18$
for imagoes,	$15.85 - 4.32 = 11.53$
for larvae-pupae,	$17.63 - 8.98 = 8.65$

These differences all have a probability value of less than 0.0000.

Between Non-parasitized Species, within Volume.—When the sterile cultures grown in the same volume are compared as to species, it is immediately apparent that removal of Adelina from both allows *T. castaneum* to attain densities very much greater than those displayed by *T. confusum* whether parasitized or not. Under these conditions, *T. castaneum* has a mean total density of 33.48 organisms per gram as against 18.94 for *T. confusum* ($P<0.0000$); a mean imaginal density of 15.85 as against 12.73 ($P = 0.0085$); and a mean larval-pupal density of 17.63 as against 6.21 ($P<0.0000$). This becomes all the more striking when it is remembered that the population levels of *T. castaneum* in the presence of infection fall significantly below that of *T. confusum*.

Percentage Composition.—Statistics describing composition in percentages for the entire period are listed in Table 12, along with comparisons of selected mean differences. Only imagoes are treated because, obviously, the percentage of larvae-pupae is readily obtained for any case by subtracting a listed figure from 100.

The findings are so straightforward that they can be quickly summarized in the following statements:

(1) *T. confusum* populations are characterized by a higher proportion of imagoes (and a lower proportion of larvae-pupae) than are *T. castaneum* populations. This is true for all volumes and for parasitized and non-parasitized cultures alike. All such differences between the two species are highly significant statistically (P ranges from 0.0012 to <0.0000).

(2) There is extremely little divergence in percentage composition between the three volumes within the species. Thus, *T. confusum* displays 48.2 per cent imagoes in 8 grams of medium, 47.2 per cent in 40 grams, and 41.1 per cent in 80 grams. Comparable figures for *T. castaneum* are 29.5, 24.9, and 28.3. Any combination of differences within the two sets of percentages are completely insignificant (P ranges from 0.1208 to >0.5).

(3) For both beetles, removal of Adelina increases the imagoes relative to the larval-pupal component to a significant degree. *T. confusum* rises from 48.2 (I-C-b) to 69.0 (I-C-b-S) and *T. castaneum* from 29.5 (I-C-c) to 48.2 (I-C-c-S). Suggestively enough, the rise in each case is in the order of 20 per cent.

VARIABILITY WITHIN AND BETWEEN CONTROL POPULATIONS

This paper is not primarily a study of population variability. Its principal objective lies in making clear the major trends exhibited by single and mixed-species cultures in order that something can be advanced regarding the phenomenon of competition under controlled laboratory conditions. An interesting, but secondary, contribution could concern itself in a comprehensive way with such variability to which the design of the program and the data lend themselves. Possibly an extension in this direction will be forthcoming. The present responsibility, however, is to briefly summarize certain facts about populations in terms of their variability that seem relevant for the central argument.

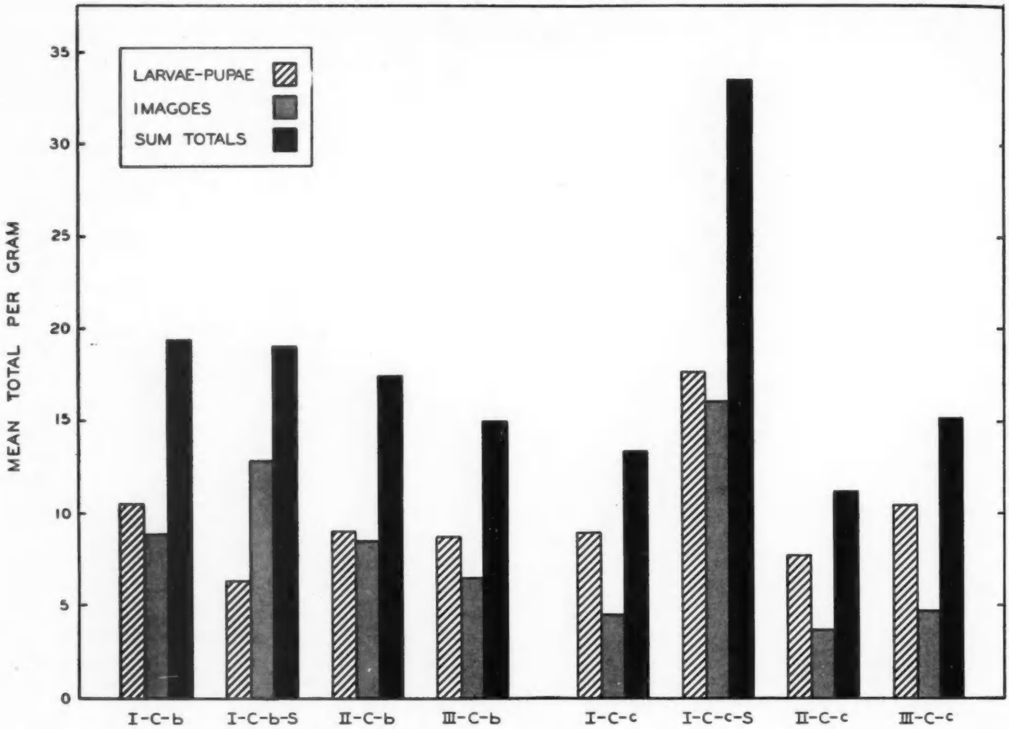

Fig. 8. Bar diagram showing the mean total population density of all eight types of control cultures averaged for the entire period of census.

This could be done in several ways. Perhaps the simplest, yet most meaningful, device would be to present graphs for the 119 control cultures whose census history has been followed and to discuss these with respect to similarities and differences. This method, however, would be too cumbersome for presentation here, although I have used it quite freely for my own edification. It would be possible also to treat the data and assay their variation by means of more elegant quantitative methods. While this may be attempted in the future, it has seemed sufficient for present purposes to rely upon such familiar statistics as the range, the standard deviation, and the coefficient of variability.

The variability displayed by each of the eight types of populations is assessed in two ways: first, for the entire period of study, and second, for eight census ages arbitrarily chosen at intervals of 150 days, beginning at day-90 (i.e., days 90, 240, 390, 540, 690, 840, 990, and 1140). The requisite figures appear in Table 10 for the grouped data, and in Table 13 for the data treated by intervals.

The Grouped Data.—Several interesting features are revealed by the ranges, standard deviations, and coefficients of variability of Table 10. First, no consistent trends are discernible for either species of beetle that can be related to volume of medium. Second, *T. confusum* in terms of total population size appears somewhat less variable, on both an absolute and relative basis, than does *T. castaneum.* This point is related, perhaps, to the greater effect exerted by Adelina on the latter beetle. Third, cultures of *T. confusum* exhibit more variation when the immature and adult components are examined individually than when the two are summed and considered together. Fourth, this same relation does not obtain with any measure of consistency for *T. castaneum.* Fifth, when the ranges are examined, it is clear that there is a greater spread between maximum and minimum values (for total population) for *T. castaneum* than for *T. confusum*, the former species thus attaining, for brief moments at least, greater and lower densities during the course of its census history. Sixth, removal of Adelina from the cultures appears to exert no systematic effect on variation beyond reducing the coefficient of variability for I-C-b-S imagoes, increasing (owing to the larger size of the cultures) the standard deviations for I-C-c-S, and lowering their coefficients.

The Data by Census Intervals.—The data are treated by census intervals for the primary purpose of seeing whether there are any marked trends of variability associated with age of cultures. This operation has been limited to mean total size and necessarily confined, because only two replicates exist

TABLE 12. Percentage imago composition for total period of study including selected statistical comparisons (30-day census excluded).

Population	Range: Maximum	Range: Minimum	Mean ± P. E.	Standard Deviation	C. V.	n	Days Observed
I-C-b	95.2	27.8	48.2±2.05	20.4	42.3	45	1350
I-C-b-S	94.9	49.6	69.0±1.33	12.0	17.4	37	1110
II-C-b	97.3	26.7	47.2±2.10	20.7	43.8	44	1320
III-C-b	97.4	17.7	41.1±2.25	22.6	55.0	46	1380
I-C-c	64.0	17.3	29.5±1.33	13.2	44.7	45	1350
I-C-c-S	63.9	33.1	48.2±0.94	8.5	17.6	37	1110
II-C-c	67.3	16.0	24.9±1.46	14.5	58.2	45	1350
III-C-c	69.6	8.6	28.3±1.47	14.8	52.3	46	1380

The Comparison	Largest Number of pair	Mean Difference ± P. E.	Probability
I-C-b and I-C-b-S	I-C-b-S	20.8±2.44	<0.0000
I-C-b and II-C-b	I-C-b	1.0±2.93	>0.5
I-C-b and III-C-b	I-C-b	7.1±3.04	0.1208
II-C-b and III-C-b	II-C-b	6.1±3.08	0.1773
I-C-c and I-C-c-S	I-C-c-S	18.7±1.63	<0.0000
I-C-c and II-C-c	I-C-c	4.6±1.97	0.1208
I-C-c and III-C-c	I-C-c	1.2±1.98	>0.5
II-C-c and III-C-c	III-C-c	3.4±2.07	0.2805
I-C-b and I-C-c	I-C-b	18.7±2.44	<0.0000
I-C-b-S and I-C-c-S	I-C-b-S	20.8±1.63	<0.0000
II-C-b and II-C-c	II-C-b	22.3±2.56	<0.0000
III-C-b and III-C-c	III-C-b	12.8±2.69	0.0012

for the two series-III groups, to series-I and II. The results are presented in Table 13.

For study purposes, the standard deviations and coefficients of variability listed in the table were plotted against age for the six types of control cultures (I-C-b, I-C-b-S, II-C-b, I-C-c, I-C-c-S, and II-C-c). The curves lie rather closely together, frequently intercross, and essentially parallel the abscissa. The major point made by these graphs, however, is that the pattern of variability does not change in any appreciable way with time. This conclusion, although a negative one, is significant for our purposes because of its implication that a conception of progressive, temporal modification of variation can be excluded. The I-C-c-S populations afford something of an exception to this generalization. In these, the standard deviations fluctuate between high and low values. Such fluctuations are usually correlated with the magnitude of the mean and are related to a matter already noted, namely: that the sterile *T. castaneum* cultures tend to build up high densities, then undergo decline leading to lower densities, then build up again, and so on.

Other suggestions emerge from inspection of Table 13, but these are of relatively minor importance and need not be pursued.

MIXED-SPECIES POPULATIONS: EXPERIMENTALS

INTRODUCTORY

In the foregoing pages attention has centered on populations of *Tribolium confusum* and *Tribolium castaneum* reared apart as *intraspecies* systems. The emphasis now shifts to *interspecies* systems for which competition between the two forms can be detected, described, and partially analyzed. It is the relation of these competitions to the fate of both species of Tribolium maintained as mixed-species groups that we now wish to explore, making frequent use of the data and interpretations presented in the section just concluded.

It will be remembered that the experimental cultures differ from the controls only in the fact that *both* species were introduced into the vials when the populations were started. Apart from this, controls and experimentals are grown in the same medium allocated in the same three volumes (I, II, III), and maintained under similar conditions of physical environment, husbandry, and laboratory handling. Table 1 lists all types of experimental cultures and clarifies their respective designs. It need only be recalled at this point that the notation E-a signifies populations in which both beetles were introduced in equal ratio; E-b signifies that *T. confusum* possessed an initial numerical advantage over *T. castaneum;* and E-c, that *T. castaneum* had a similar advantage over *T. confusum*. In order to round out the total investigation, non-parasitized or "sterile" cultures were started, having the constitution I-E-a-S, and these will be considered later as a special case.

FINAL CONSEQUENCES OF COMPETITION

Before discussing in some detail each type of experimental culture, it is helpful to make clear just what is the final consequence, or end-result, of com-

TABLE 13. Variability of six control populations assayed for eight census periods at intervals of 150 days.

Age (days)	Population	Mean ± P. E. (per gram)	Standard Deviation (per gram)	Coefficient of Variability (per cent)	n
90	I-C-b	22.19± 0.9304	6.17	27.8	20
	I-C-b-S	25.1 ± 0.6439	4.27	17.0	20
	II-C-b	24.8 ± 0.3288	2.01	8.1	17
	I-C-c	29.3 ± 0.9938	6.59	22.5	20
	I-C-c-S	35.2 ± 0.7570	5.02	14.3	20
	II-C-c	30.0 ± 0.5295	3.33	11.1	18
240	I-C-b	17.1 ± 0.7600	5.04	29.5	20
	I-C-b-S	17.4 ± 0.4614	3.06	17.6	20
	II-C-b	18.0 ± 0.3697	2.26	12.5	17
	I-C-c	12.6 ± 0.7842	5.20	41.6	20
	I-C-c-S	50.3 ± 3.8716	24.35	48.4	18
	II-C-c	10.8 ± 0.6074	3.82	35.4	18
390	I-C-b	15.8 ± 0.8263	5.48	34.8	20
	I-C-b-S	16.9 ± 0.4451	2.64	15.6	17
	II-C-b	14.8 ± 0.5971	3.65	24.7	17
	I-C-c	12.1 ± 1.0622	6.30	52.1	16
	I-C-c-S	23.3 ± 1.1114	6.99	30.0	18
	II-C-c	10.9 ± 0.5535	3.48	31.9	18
540	I-C-b	15.2 ± 0.7102	4.71	30.9	20
	I-C-b-S	21.7 ± 0.7890	4.68	21.6	17
	II-C-b	15.7 ± 0.4368	2.67	17.0	17
	I-C-c	10.2 ± 0.6473	3.59	35.2	14
	I-C-c-S	44.4 ± 2.4629	15.49	34.9	18
	II-C-c	9.1 ± 0.2417	1.52	16.7	18
690	I-C-b	18.6 ± 1.2893	8.55	45.9	20
	I-C-b-S	18.2 ± 0.4231	2.51	13.8	16
	II-C-b	15.4 ± 0.4024	2.46	16.0	17
	I-C-c	12.6 ± 0.9467	5.06	40.5	13
	I-C-c-S	25.3 ± 0.8867	5.42	21.4	17
	II-C-c	8.2 ± 0.3482	2.19	26.7	18
840	I-C-b	19.4 ± 0.7193	4.65	23.9	19
	I-C-b-S	20.8 ± 0.6946	4.12	19.8	16
	II-C-b	14.8 ± 0.5955	3.64	24.6	17
	I-C-c	13.4 ± 0.7652	4.09	30.5	13
	I-C-c-S	47.2 ± 2.1345	12.66	26.8	16
	II-C-c	7.2 ± 0.2353	1.48	20.5	18
990	I-C-b	19.5 ± 0.7131	4.61	23.6	19
	I-C-b-S	15.9 ± 0.3344	1.92	12.1	15
	II-C-b	17.4 ± 0.3763	2.30	13.2	17
	I-C-c	15.0 ± 1.2311	6.58	44.2	13
	I-C-c-S	21.1 ± 1.0882	5.35	25.4	11
	II-C-c	9.2 ± 0.3482	2.19	23.8	18
1140	I-C-b	22.6 ± 0.8059	5.21	23.1	19
	I-C-b-S	18.6 ± 0.5870	3.37	18.1	15
	II-C-b	16.9 ± 0.3877	2.37	14.0	17
	I-C-c	11.0 ± 0.8270	4.42	40.2	13
	I-C-c-S	27.4 ± 1.1600	5.16	18.8	9
	II-C-c	8.1 ± 0.6471	4.07	50.2	18

petition as this relates to the fate of populations of both beetles. It has been shown that the control cultures, free of interspecies complications, eventually assume characteristic "equilibria" that are sustained for relatively long periods of time in terms of number of generations.

The major ecological finding of this entire study can be simply stated as follows: when *T. confusum* and *T. castaneum* are brought into competition, one of the two invariably becomes extinct with the other then assuming its "normal" (i.e., control) populational behavior. To put it differently, in the face of such stringent competition, it becomes impossible for both species to co-exist even though individually they are well adapted to their habitat and its surrounding physical environment.

Despite the fact that one species of Tribolium always becomes extinct in this two-species ecosystem, it is not always the *same* species that dies out. By examining what happens to each of the 92 experimental populations, it is a simple matter to tabulate which species dies along with the census age at which this occurs. These findings are systematically presented in Table 14. In certain instances, *T. confusum* became extinct in some populations, while *T. castaneum* disappeared in others. This is noted in the third column of the table under the heading "species becoming extinct." The last two columns list the mean and median ages of extinction.

From inspection of Table 14, the following points, all pertaining to species extinction, are to be noted:

(1) For the I-E-a populations consisting of 15 replicates, there are 11 cases of extinction of *T. castaneum* and 4 of *T. confusum*.

(2) For the I-E-c populations consisting, again, of 15 replicates, there are, again, 11 cases of extinction of *T. castaneum* and 4 of *T. confusum*.

(3) For the I-E-b populations, *T. castaneum* dies out in all of the 15 cultures.

(4) For the II and III series, totaling 29 populations, *T. castaneum* always becomes extinct whether the cultures are in the E-a, E-b, or E-c categories. Thus, 29 populations, originally established as mixed-species groups, eventually wound up as single-species cultures of *T. confusum*.

(5) When Adelina is removed and 18 sterile populations are established (I-E-a-S) the trend is reversed with *T. castaneum* typically winning over *T. confusum*. The former is successful in 12 out of 18 replicates.

The major conclusions emerging from the above summary are (a) that both species of beetles cannot live together for any extended period, and (b) that, in competition, *T. castaneum* characteristically disappears, with *T. confusum* remaining as the successful organism. The last event happens much more frequently than would be expected on the hypothesis that it is a matter of equal chance as to which species survives. Excluding for the moment the sterile cultures, Table 14 shows that from a group of 74 populations there are only 8 instances in which *T. confusum* becomes extinct, to be compared with 66 instances for which the reverse is true. This ratio differs significantly from the 37:37 distribution anticipated on an assumption of 50:50.

Accordingly, we are left with the not unreasonable conception that, in the presence of the parasite Adelina, a particular species of flour beetle characteristically survives in a competing system but that this does not invariably hold true, while, when the parasite is eliminated as a factor, the usual trend just described is reversed, although this, too, has its exceptions. In short, it is possible to predict the

most probable outcome of interspecies competition for a particular experimental series, but this is not an all-or-none phenomenon since reversals sometime take place. These matters receive further attention later after each type of population has been reviewed in some detail.

The mixed-species populations.—The basic findings pertaining to competition between *Tribolium confusum* and *T. castaneum* will be presented by considering the following topics:

(1) Parasitized populations in which *T. castaneum* always becomes extinct.
(2) Extinction curves for *T. castaneum* and *T. confusum* compared.
(3) Extinction of *T. castaneum* and *T. confusum* in the absence of Adelina.

The data dealing with the mixed-species populations are presented as a series of tables and graphs similarly designed throughout. Two tables and graphs are required for each of the I-E-a, I-E-c, and I-E-a-S populations to record the fact that in these cultures certain replicates lost all their *T. castaneum* and became *T. confusum* controls, while in others the opposite occurred.

Each table reports census figures for both species of Tribolium as mean number per gram and as percentages of total size. The data are tabulated by 30 day periods along with which is shown, as the *n*-column, that number of replicates remaining as experimental cultures. For example, in Table 15 there are nine populations making up the sample at day-360 of which only six remain at day-390. In other words, three populations have become controls during the interval between censuses.

In all tables, the number of larvae-pupae is recorded both as a total and as species components of that total. While the former statistic is accurately determined by counting, the breakdown by species is necessarily based on computation rather than on census simple because the immature stages cannot be taxonomically identified. However, it seems logical to assume that the ratio between larvae-pupae and imagoes for each species in the experimentals is essentially the same as in the populations of single species (controls). Since this ratio is known for the controls it is possible to calculate the number of larvae-pupae in the experimentals that are probably *T. confusum* and those that are probably *T. castaneum*.[5]

The figures are graphed to stress competition between the species and hence, may be referred to as "competition curves." The ordinate plots the "total percentage of *T. castaneum*" (third column from the right in the tables) and the abscissa, "age in days." The distance from the abscissa to the curve denotes that percentage of the total population which is *T. castaneum;* the distance from the curve to the one-hundred per cent line denotes the percentage of *T. confusum*. Each figure shows at a glance the relative proportion of the two species at any census age. When the curve drops, *T. confusum* is increasing; and if the curve falls to the baseline, the populations have become *T. confusum* controls. When the curve reaches the top horizontal line, as happens in some of the Series I cultures, the populations have become exclusively *T. castaneum*.

In inspecting the various graphs, it should be kept in mind that, as the sample gets older, individual populations are dropping out through extinction of one of the two species. In other words, the points plotted in every figure are based on progressively fewer observations (cultures) until, eventually, only the life-history of one experimental culture remains to be depicted. From one point of view, this is an unfortunate method of representing the data in that reduction in number of cases obviously decreases in a measure the reliability of the curves during their later periods. On the other hand, the alternative method of graphing is less desirable. It is unrealistic to arbitrarily set as temporally equal for all replicates the census ages at which the expiring species was last counted, thus ignoring the chronology of the extinction, and then draw the curves backward in time from this assumed origin. Such a procedure was tried extensively in study graphs but forsaken because of the wide age-range within which species extinction can occur between different replicates. Also, the knowledge at our disposal about the trends exhibited by control cultures makes it clear that it is not legitimate to consider an experimental population of the age of, say, 180 days, to be ecologically equivalent with an-

[5] A note on the method is appropriate. For every census these data are available: total population size, number of *T. castaneum* imagoes, number of *T. confusum* imagoes, total number of larvae-pupae undifferentiated as to species, and percentages of larvae-pupae (and imagoes) in control cultures of both species for any desired age. These data can be utilized in differentiating the total number of larvae-pupae into its species components. Letting "b" symbolize *T. confusum* and "c" *T. castaneum*, the steps in the solution are as follows:

$$(1)\quad \frac{\text{c-imagoes}\left(\dfrac{\%\text{ larvae-pupae in c-controls}}{\%\text{ imagoes in c-controls}}\right)}{\text{b-imagoes}\left(\dfrac{\%\text{ larvae-pupae in b-controls}}{\%\text{ imagoes in b-controls}}\right)} = \frac{X}{Y}$$

$$(2)\quad \frac{X\text{ (observed total larvae-pupae)}}{(X + Y)} = \text{calculated larvae-pupae } (\textit{T. castaneum})$$

$$(3)\quad \frac{Y\text{ (observed total larvae-pupae)}}{(X + Y)} = \text{calculated larvae-pupae } (\textit{T. confusum})$$

Suppose this is applied to an actual case, e.g., the 300-day census for I-E-a reported in Table 15. There the total population is 13.0; number of b-imagoes is 3.7 and c-imagoes 0.8; total larvae-pupae, 8.5; per cent larvae-pupae at day-300 in I-C-b is 46% (from Table 2) and in I-C-c is 80 % (from Table 5).

Substituting,

$$(1)\quad \frac{0.8\left(\dfrac{80}{20}\right)}{3.7\left(\dfrac{46}{54}\right)} = \frac{3.2}{3.1}$$

$$(2)\quad \frac{(3.2)\ (8.5)}{(6.3)} = 4.3\ (\textit{T. castaneum}\text{ larvae-pupae})$$

$$(3)\quad \frac{(3.1)\ (8.5)}{(6.3)} = 4.2\ (\textit{T. confusum}\text{ larvae-pupae})$$

I am indebted to Mr. Thomas Burnett of the University of Chicago for originally suggesting this method and to Doctor Margaret Merrill of the Johns Hopkins University and Doctor L. C. Cole of Indiana University for advising me as to its appropriateness.

TABLE 14. Age at extinction for each of the 92 mixed-species populations.

Experimental Type	Total Number of Replicates	Species Becoming Extinct: Species	Species Becoming Extinct: Frequency	Age at Extinction of Individual Populations (Days)	Averages (Days): Mean	Averages (Days): Median
I-E-a	15	*T. castaneum*	11	270, 360, 390, 390, 390, 570, 600, 600, 630, 630, 780.	510±30.3	570±38.0
		T. confusum	4	510, 630, 690, 780.	652	660
II-E-a	9	*T. castaneum*	9	300, 360, 360, 390, 420, 420, 660, 690, 1020.	513±49.5	420±62.0
		T. confusum	0			
III-E-a	2	*T. castaneum*	2	840, 1470.		
		T. confusum	0			
I-E-a-S	18	*T. castaneum*	6	210, 270, 270, 360, 360, 450.	320±21.8	315±27.3
		T. confusum	12	510, 540, 570, 600, 600, 660, 660, 690, 690, 810, 810, 840.	665±20.2	660±25.3
I-E-b	15	*T. castaneum*	15	270, 300, 300, 300, 330, 360, 360, 360, 390, 390, 450, 600, 630, 720, 750.	434±26.8	360±33.4
		T. confusum	0			
II-E-b	7	*T. castaneum*	7	300, 330, 330, 360, 420, 450, 540.	390±20.1	360±25.2
		T. confusum	0			
III-E-b	2	*T. castaneum*	2	330, 360.	345	345
		T. confusum	0			
I-E-c	15	*T. castaneum*	11	330, 330, 360, 390, 390, 390, 450, 450, 510, 600, 600.	436±19.1	390±23.9
		T. confusum	4	180, 420, 540, 690.	458	480
II-E-c	7	*T. castaneum*	7	330, 390, 450, 480, 540, 690, 930.	549±46.9	480±58.8
		T. confusum	0			
III-E-c	2	*T. castaneum*	2	750, 810.	780	780
		T. confusum	0			

other population 840 days old, even though the two were started simultaneously under initially similar conditions.

Therefore, the number of cases used in computing the points has been sacrificed in order to maintain a strict chronology of events for both control and experimental cultures. This is probably not as serious as might be suspected at first glance because (1) the age of species extinction is accurately known for each culture, and (2) there is a general consistency between homologous figures that is quite reassuring.

Parasitized Populations in Which Tribolium castaneum Becomes Extinct

This category, involving the extinction of populations of *T. castaneum* when in competition with *T. confusum*, encompasses the majority (i.e., 66 out of 74) of the experimental cultures reported upon in this paper. The findings are presented by discussing the following sets of experiments in the order indicated:

(1) I-E-a, II-E-a, III-E-a
(2) I-E-b, II-E-b, III-E-b
(3) I-E-c, II-E-c, III-E-c
(4) General conclusions and comparisons between E-a, E-b, and E-c

The requisite data are contained in Tables 15 through 23, and selected competition curves are graphed as Figures 9, 10, and 11.

I-E-a, II-E-a, and III-E-a populations.—The feature that immediately strikes the eye when Figure 9 is examined is the essential conformity displayed by the three curves—curves summarizing experiments which differ in their design only in terms of volume of medium. *T. castaneum* attains its maximum abundance at day-90 when 80 per cent of the entire population is composed of this species. Thus, from an initial seeding of one-half *T. castaneum* to one-half *T. confusum*, the former increases at the expense of the latter until it occupies over three-fourths of the total habitat. This occurs early in the cultures' history despite the fact that it is *T. castaneum* that is definitely going to become extinct at a series of later dates! Reference to Tables 5, 6, and 7 will indicate that the 90-day census is also a large one for I-C-c, II-C-c, and III-C-c populations.

Returning to Figure 9, it is evident that the drop in percentage of *T. castaneum* starts at day-120, proceeds slowly for a time, and then accelerates. Between days-240 and 270 most of the cultures reach the 50 per cent line, and by day-360 the situation has so changed that now *T. confusum* constitutes something like 85 to 90 per cent of the total. It seems reasonable that much of this decline during the 90-360 day interval is conditioned, not primarily by competitive pressure exerted by *T. confusum*, but, rather, by the increase and spread of Adelina infection with its consequent and now well-known adverse effects upon *T. castaneum*. A decline is seen in the control cultures (I-C-c, II-C-c, and III-C-c) that is quite like that depicted in Figure 9, both in respect of magnitude and age interval of occurrence. The control cultures, of course, then proceed to recover[6] while *T. castaneum* in the experimental cultures does not.

[6] With the exception of the eight I-C-c populations discussed earlier in the section devoted to controls.

TABLE 15. I-E-a: *Tribolium castaneum* becoming extinct.

Age (days)	Mean Number Per Gram									Percentage of						n
	T. castaneum			*T. confusum*			Total			Larvae and Purae		Imagoes		Total		
	L-P	Imag.	Sum	L-P	Imag.	Sum	L-P	Imag.	Sum	*T. cast.*	*T. conf.*	*T. cast.*	*T. conf.*	*T. cast.*	*T. conf.*	
30	3.9	1.6	5.5	6.6	0.9	7.5	10.5	2.5	13.0	30.0	50.8	12.3	6.9	42.3	57.7	11
60	4.9	9.4	14.3	1.1	5.2	6.3	6.0	14.6	20.6	23.8	5.3	45.6	25.3	69.4	30.6	11
90	14.3	9.2	23.5	0.9	4.9	5.8	15.2	14.1	29.3	48.8	3.1	31.4	16.7	80.2	19.8	11
120	7.7	8.1	15.8	0.4	4.5	4.9	8.1	12.6	20.7	37.2	1.9	39.1	21.8	76.3	23.7	11
150	6.5	7.2	13.7	0.3	4.3	4.6	6.8	11.5	18.3	35.5	1.6	39.4	23.5	74.9	25.1	11
180	5.9	5.7	11.6	0.6	3.9	4.5	6.5	9.6	16.1	36.6	3.7	35.4	24.3	72.0	28.0	11
210	4.8	3.4	8.2	1.0	3.7	4.7	5.8	7.1	12.9	37.2	7.7	26.4	28.7	63.6	36.4	11
240	6.5	2.4	8.9	2.4	3.4	5.8	8.9	5.8	14.7	44.2	16.3	16.4	23.1	60.6	39.4	11
270	4.9	1.6	6.5	2.2	3.3	5.5	7.1	4.9	12.0	40.8	18.3	13.4	27.5	54.2	45.8	10
300	4.3	0.8	5.1	4.2	3.7	7.9	8.5	4.5	13.0	33.1	32.3	6.1	28.5	39.2	60.8	10
330	3.6	0.6	4.2	5.7	4.7	10.4	9.3	5.3	14.6	24.7	39.0	4.1	32.2	28.8	71.2	10
360	1.1	0.5	1.6	6.1	5.8	11.9	7.2	6.3	13.5	8.1	45.2	3.8	42.9	11.9	88.1	9
390	2.4	0.8	3.2	4.9	4.9	9.8	7.3	5.7	13.0	18.5	37.7	6.1	37.7	24.6	75.4	6
420	2.2	0.7	2.9	5.5	5.3	10.8	7.7	6.0	13.7	16.1	40.1	5.1	38.7	21.2	78.8	6
450	1.0	0.3	1.3	7.2	5.6	12.8	8.2	5.9	14.1	7.1	51.1	2.1	39.7	9.2	90.8	6
480	1.7	0.6	2.3	6.1	5.8	11.9	7.8	6.4	14.2	12.0	43.0	4.2	40.8	16.2	83.8	6
510	1.3	0.5	1.8	5.4	6.3	11.7	6.7	6.8	13.5	9.6	40.0	3.7	46.7	13.3	86.7	6
540	1.0	0.4	1.4	8.1	6.0	14.1	9.1	6.4	15.5	6.4	52.3	2.6	38.7	9.0	91.0	6
570	0.8	0.3	1.1	7.2	6.1	13.3	8.0	6.4	14.4	5.5	50.0	2.1	42.4	7.6	92.4	5
600	1.2	0.3	1.5	8.1	5.3	13.4	9.3	5.6	14.9	8.0	54.4	2.1	35.5	10.1	89.9	3
630	2.5	0.5	3.0	5.8	3.8	9.6	8.3	4.3	12.6	19.8	46.0	4.0	30.2	23.8	76.2	1
660	0.9	0.2	1.1	6.5	3.8	10.3	7.4	4.0	11.4	7.9	57.0	1.8	33.3	9.7	90.3	1
690	1.0	0.1	1.1	9.8	4.0	13.8	10.8	4.1	14.9	6.7	65.8	0.7	26.8	7.4	92.6	1
720	0.5	0.1	0.6	12.6	4.9	17.5	13.1	5.0	18.1	2.8	69.6	0.5	27.1	3.3	96.7	1
750	0.5	0.1	0.6	14.5	5.9	20.4	15.0	6.0	21.0	2.4	69.0	0.5	28.1	2.9	97.1	1

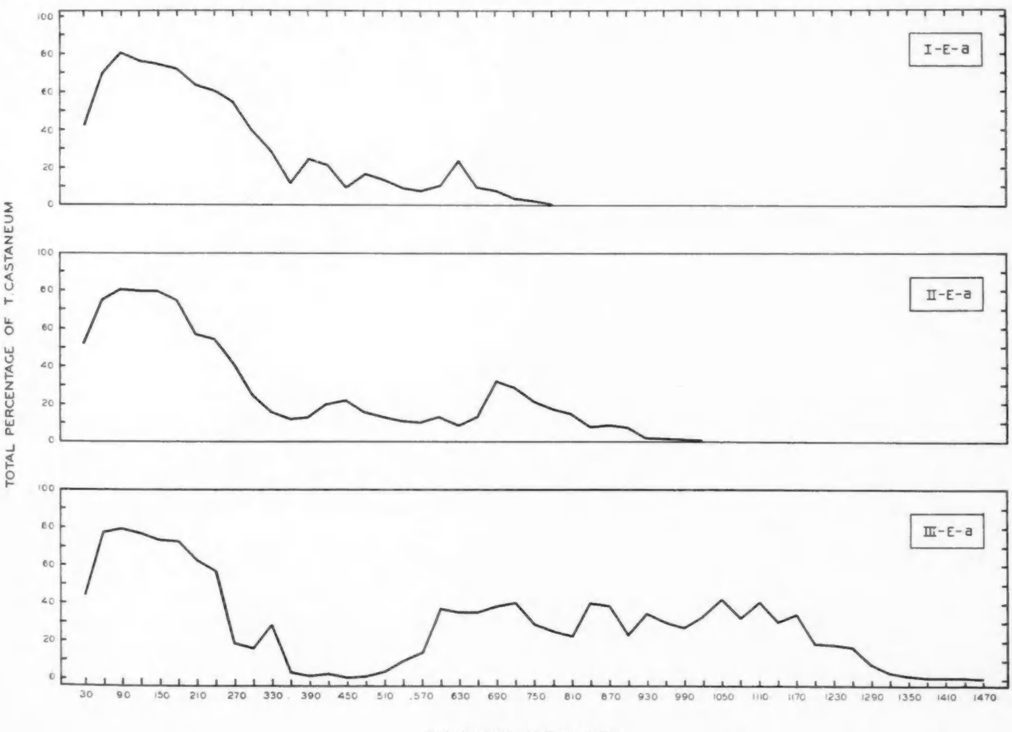

FIG. 9. Competition curves (percentage of *T. castaneum* against age in days) for I-E-a, II-E-a, and III-E-a populations in which *T. castaneum* eventually becomes extinct. (Distance from abscissa to curve is that percentage of the total count which is *T. castaneum*; from curve to 100 per cent line, the percentage of *T. confusum*.)

TABLE 16. II-E-a: *Tribolium castaneum* becoming extinct.

Age (days)	Mean Number Per Gram									Percentage of						n
	T. castaneum			*T. confusum*			Total			Larvae and Pupae		Imagoes		Total		
	L-P	Imag.	Sum	L-P	Imag.	Sum	L-P	Imag.	Sum	*T. cast.*	*T. conf.*	*T. cast.*	*T. conf.*	*T. cast.*	*T. conf.*	
30	7.2	3.8	11.0	9.2	1.0	10.2	16.4	4.8	21.2	34.0	43.4	17.9	4.7	51.9	48.1	9
60	6.7	11.3	18.0	1.1	5.0	6.1	7.8	16.3	24.1	27.8	4.6	46.9	20.7	74.7	25.3	9
90	9.0	11.2	20.2	0.4	4.6	5.0	9.4	15.8	25.2	35.7	1.6	44.5	18.2	80.2	19.8	9
120	7.6	10.1	17.7	0.1	4.5	4.6	7.7	14.6	22.3	34.1	0.4	45.3	20.2	79.4	20.6	9
150	7.6	8.4	16.0	0.1	4.1	4.2	7.7	12.5	20.2	37.6	0.5	41.6	20.3	79.2	20.8	9
180	6.1	5.3	11.4	0.3	3.6	3.9	6.4	8.9	15.3	39.9	2.0	34.6	23.5	74.5	25.5	9
210	4.0	1.8	5.8	1.2	3.2	4.4	5.2	5.0	10.2	39.2	11.8	17.7	31.3	56.9	43.1	9
240	5.8	0.9	6.7	2.2	3.5	5.7	8.0	4.4	12.4	46.8	17.7	7.2	28.3	54.0	46.0	9
270	5.0	0.5	5.5	3.9	3.9	7.8	8.9	4.4	13.3	37.6	29.3	3.8	29.3	41.4	58.6	9
300	2.9	0.4	3.3	5.3	5.1	10.4	8.2	5.5	13.7	21.2	38.7	2.9	37.2	24.1	75.9	8
330	1.9	0.3	2.2	6.8	5.6	12.4	8.7	5.9	14.6	13.0	46.6	2.1	38.3	15.1	84.9	8
360	1.1	0.3	1.4	4.7	5.9	10.6	5.8	6.2	12.0	9.2	39.2	2.5	49.1	11.7	88.3	6
390	1.4	0.3	1.7	6.9	4.7	11.6	8.3	5.0	13.3	10.5	51.9	2.3	35.3	12.8	87.2	5
420	1.8	0.4	2.2	5.1	3.9	9.0	6.9	4.3	11.2	16.1	45.5	3.5	34.9	19.6	80.4	3
450	2.5	0.5	3.0	6.5	4.6	11.1	9.0	5.1	14.1	17.7	46.1	3.6	32.6	21.3	78.7	3
480	1.7	0.5	2.2	6.5	5.7	12.2	8.2	6.2	14.4	11.8	45.1	3.5	39.6	15.3	84.7	3
510	1.2	0.4	1.6	5.8	5.4	11.2	7.0	5.8	12.8	9.4	45.3	3.1	42.2	12.5	87.5	3
540	1.0	0.3	1.3	6.4	5.1	11.5	7.4	5.4	12.8	7.8	50.0	2.4	39.8	10.2	89.8	3
570	0.9	0.3	1.2	5.9	5.2	11.1	6.8	5.5	12.3	7.3	50.0	2.5	40.2	9.8	90.2	3
600	1.3	0.3	1.6	5.9	5.1	11.0	7.2	5.4	12.6	10.3	46.8	2.4	40.5	12.7	87.3	3
630	0.8	0.2	1.0	6.2	5.3	11.5	7.0	5.5	12.5	6.4	49.6	1.6	42.4	8.0	92.0	3
660	1.3	0.5	1.8	6.6	5.6	12.2	7.9	6.1	14.0	9.3	47.1	3.6	40.0	12.9	87.1	2
690	3.2	0.8	4.0	4.8	3.7	8.5	8.0	4.5	12.5	25.6	38.4	6.4	29.6	32.0	68.0	1
720	3.2	0.8	4.0	6.5	3.6	10.1	9.7	4.4	14.1	22.7	46.1	5.7	25.5	28.4	71.6	1
750	2.3	0.6	2.9	7.1	3.7	10.8	9.4	4.3	13.7	16.8	51.8	4.4	27.0	21.2	78.8	1
780	2.1	0.5	2.6	8.9	3.7	12.6	11.0	4.2	15.2	13.8	58.5	3.3	24.4	17.1	82.9	1
810	1.9	0.4	2.3	9.4	4.5	13.9	11.3	4.9	16.2	11.7	58.0	2.5	27.8	14.2	85.8	1
840	0.9	0.2	1.1	8.9	4.0	12.9	9.8	4.2	14.0	6.4	63.6	1.5	28.5	7.9	92.1	1
870	0.6	0.3	0.9	5.3	4.6	9.9	5.9	4.9	10.8	5.6	49.1	2.7	42.6	8.3	91.7	1
900	1.0	0.2	1.2	10.7	4.2	14.9	11.7	4.4	16.1	6.2	66.5	1.3	26.0	7.5	92.5	1
930	0.2	0.05	0.25	10.3	5.95	16.25	10.5	6.0	16.5	1.2	62.4	0.3	36.1	1.5	98.5	1
960	0.1	0.05	0.15	8.4	6.72	15.12	8.5	6.77	15.27	0.6	55.0	0.4	44.0	1.0	99.0	1
990	0.1	0.02	0.12	9.2	6.55	15.75	9.3	6.57	15.87	0.6	58.0	0.2	41.2	0.8	99.2	1

Despite their fundamental similarity, there are also certain differences between the graphs of Figure 9—differences especially evident after the first year—and these require mention. While the I-E-a and II-E-a populations are themselves reasonably confluent, both diverge somewhat from III-E-a. For one thing, the III-E-a curve falls much lower at the 360 day reading, and the two replicates are maintained as experimental cultures only by virtue of the presence of a very few *T. castaneum* (0.5 to 3.8%). After day-540, however, this species stages so sharp a recovery that it returns to a level quite higher than that seen in the populations of smaller volumes. This is well documented by noting that, over the twenty census readings starting at day-600 and ending at day-1170, *T. castaneum* constitutes, on the average, 34% of the total. It is a possible conjecture that this increase is related to a temporary reduction in the extent and/or effectiveness of parasitization. Figure 9 shows also that the two III-E-a cultures display a longer life-duration as experimental populations than those of the I and II volumes. In fact, these are the most longevous of all the mixed species groups. The explanation of this, if not to be accounted for by accidents of sampling, is obscure.

I-E-b, II-E-b, and III-E-b populations.—Curves depicting these three sets of cultures are graphed in Figure 10 and are based on the information contained in Tables 18, 19, and 20. Here again, a general visual similarity is evident for the three curves, particularly during the first year of growth. Also, there are clear differences in pattern between them and those describing the E-a populations (Figure 9).

The early disparity existing between the E-a and E-b series is unquestionably related to the densities in which the two species of beetles were introduced when the experiments were started. In the E-a group, in which *T. confusum* and *T. castaneum* were associated in similar numbers, the latter attained greater abundance than the former during the first three months. In the E-b group, on the other hand, *T. confusum,* introduced at a numerical advantage of 50%, was just able to maintain itself on an equal basis with its competitor during this interval. For the E-c cultures, with *T. castaneum* constituting three-fourths of the initial population, *T. confusum* multiplied only slightly during the period and occupied less than ten per cent of the total habitat at day-90. In short, there is a positive relationship between initial concentration and size of population at the time of the third census, but *T. castaneum* takes greater advantage of this than does *T. confusum* in

TABLE 17. III-E-a: *Tribolium castaneum* becoming extinct.

Age (days)	Mean Number Per Gram									Percentage of						n
	T. castaneum			*T. confusum*			Total			Larvae and Pupae		Imagoes		Total		
	L-P	Imag.	Sum	L-P	Imag.	Sum	L-P	Imag.	Sum	*T. cast.*	*T. conf.*	*T. cast.*	*T. conf.*	*T. cast.*	*T. conf.*	
30	6.7	2.9	9.6	11.0	0.9	11.9	17.7	3.8	21.5	31.2	51.2	13.5	4.1	44.7	55.3	2
60	6.0	9.9	15.9	0.6	3.9	4.5	6.6	13.8	20.4	29.4	2.9	48.5	19.2	77.9	22.1	2
90	8.3	9.6	17.9	0.1	4.5	4.6	8.4	14.1	22.5	36.9	0.4	42.7	20.0	79.6	20.4	2
120	5.7	8.9	14.6	0.1	4.2	4.3	5.8	13.1	18.9	30.2	0.5	47.1	22.2	77.3	22.7	2
150	4.4	6.8	11.2	0.2	3.8	4.0	4.6	10.6	15.2	28.9	1.3	44.8	25.0	73.7	26.3	2
180	6.1	4.9	11.0	0.7	3.4	4.1	6.8	8.3	15.1	40.4	4.6	32.5	22.5	72.9	27.1	2
210	4.7	2.2	6.9	1.2	2.9	4.1	5.9	5.1	11.0	42.7	10.9	20.0	26.4	62.7	37.3	2
240	5.4	1.1	6.5	1.9	3.0	4.9	7.3	4.1	11.4	47.4	16.7	9.6	26.3	57.0	43.0	2
270	1.9	0.3	2.2	5.8	4.0	9.8	7.7	4.3	12.0	15.8	48.3	2.5	33.4	18.3	81.7	2
300	1.9	0.2	2.1	5.6	5.5	11.1	7.5	5.7	13.2	14.4	42.4	1.5	41.7	15.9	84.1	2
330	3.4	0.8	4.2	4.4	6.3	10.7	7.8	7.1	14.9	22.8	29.5	5.4	42.3	28.2	71.8	2
360	0.59	0.06	0.65	10.91	5.78	16.69	11.50	5.84	17.34	3.4	62.9	0.4	33.3	3.8	96.2	2
390	0.18	0.02	0.20	10.42	4.37	14.79	10.60	4.39	14.99	1.2	69.5	0.1	29.2	1.3	98.7	2
420	0.42	0.02	0.44	15.67	3.79	19.46	16.09	3.81	19.90	2.1	78.7	0.1	19.1	2.2	97.8	2
450	0.08	0.01	0.09	12.03	4.87	16.90	12.11	4.88	16.99	0.4	70.8	0.1	28.7	0.5	99.5	2
480	0.14	0.03	0.17	10.67	6.12	16.79	10.81	6.15	16.96	0.8	62.9	0.2	36.1	1.0	99.0	2
510	0.69	0.06	0.75	14.51	4.51	19.02	15.20	4.57	19.77	3.5	73.4	0.3	22.8	3.8	96.2	2
540	1.3	0.2	1.5	10.5	4.1	14.6	11.8	4.3	16.1	8.1	65.2	1.2	25.5	9.3	90.7	2
570	1.6	0.2	1.8	8.6	3.0	11.6	10.2	3.2	13.4	11.9	64.2	1.5	22.4	13.4	86.6	2
600	4.5	0.4	4.9	6.0	2.3	8.3	10.5	2.7	13.2	34.1	45.4	3.0	17.5	37.1	62.9	2
630	5.3	0.3	5.6	8.3	2.0	10.3	13.6	2.3	15.9	33.3	52.2	1.9	12.6	35.2	64.8	2
660	4.2	0.6	4.8	6.3	2.4	8.7	10.5	3.0	13.5	31.1	46.7	4.5	17.7	35.6	64.4	2
690	5.2	0.5	5.7	7.3	1.7	9.0	12.5	2.2	14.7	35.4	49.7	3.4	11.5	38.8	61.2	2
720	4.5	0.5	5.0	5.8	1.5	7.3	10.3	2.0	12.3	36.6	47.1	4.1	12.2	40.7	59.3	2
750	3.8	0.4	4.2	8.3	1.9	10.2	12.1	2.3	14.4	26.4	57.6	2.8	13.2	29.2	70.8	2
780	3.7	0.3	4.0	10.3	1.4	11.7	14.0	1.7	15.7	23.6	65.6	1.9	8.9	25.5	74.5	2
810	2.4	0.2	2.6	7.7	1.1	8.8	10.1	1.3	11.4	21.0	67.5	1.8	9.7	22.8	77.2	2
840	3.5	0.7	4.2	5.3	0.8	6.1	8.8	1.5	10.3	34.0	51.5	6.8	7.7	40.8	59.2	1
870	2.9	1.2	4.1	5.0	1.4	6.4	7.9	2.6	10.5	27.6	47.6	11.5	13.3	39.1	60.9	1
900	2.7	0.8	3.5	10.2	1.0	11.2	12.9	1.8	14.7	18.4	69.4	5.4	6.8	23.8	76.2	1
930	2.3	1.9	4.2	5.6	2.2	7.8	7.9	4.1	12.0	19.2	46.7	15.8	18.3	35.0	65.0	1
960	4.6	1.1	5.7	11.6	1.4	13.0	16.2	2.5	18.7	24.6	62.0	5.9	7.5	30.5	69.5	1
990	1.1	1.2	2.3	4.5	1.6	6.1	5.6	2.8	8.4	13.1	53.6	14.3	19.0	27.4	72.6	1
1020	3.7	0.8	4.5	7.8	1.2	9.0	11.5	2.0	13.5	27.4	57.8	5.9	8.9	33.3	66.7	1
1050	5.0	0.8	5.8	6.7	1.2	7.9	11.7	2.0	13.7	36.5	48.9	5.8	8.8	42.3	57.7	1
1080	3.1	0.5	3.6	6.4	1.0	7.4	9.5	1.5	11.0	28.2	58.2	4.5	9.1	32.7	67.3	1
1110	3.3	0.6	3.9	4.7	0.9	5.6	8.0	1.5	9.5	34.7	49.5	6.4	9.4	41.1	58.9	1
1140	2.1	0.4	2.5	4.9	0.8	5.7	7.0	1.2	8.2	25.6	59.8	4.9	9.7	30.5	69.5	1
1170	3.1	0.5	3.6	5.5	1.3	6.8	8.6	1.8	10.4	29.8	52.9	4.8	12.5	34.6	65.4	1
1200	2.4	0.3	2.7	9.9	1.6	11.5	12.3	1.9	14.2	16.9	69.7	2.1	11.3	19.0	81.0	1
1230	1.9	0.2	2.1	7.7	1.5	9.2	9.6	1.7	11.3	16.8	68.1	1.8	13.3	18.6	81.4	1
1260	2.3	0.2	2.5	10.5	1.6	12.1	12.8	1.8	14.6	15.7	71.9	1.4	11.0	17.1	82.9	1
1290	0.8	0.2	1.0	10.2	1.3	11.5	11.0	1.5	12.5	6.4	81.6	1.6	10.4	8.0	92.0	1
1320	0.4	0.1	0.5	12.8	2.4	15.2	13.2	2.5	15.7	2.5	81.5	0.7	15.3	3.2	96.8	1
1350	0.26	0.05	0.31	14.64	1.79	16.43	14.90	1.84	16.74	1.5	87.4	0.4	10.7	1.9	98.1	1
1380	0.08	0.02	0.10	12.52	2.24	14.76	12.60	2.26	14.86	0.5	84.2	0.2	15.1	0.7	99.3	1
1410	0.08	0.01	0.09	17.83	1.75	19.58	17.91	1.76	19.67	0.4	90.6	0.1	8.9	0.5	99.5	1
1440	0.07	0.01	0.08	20.33	1.94	22.27	20.40	1.95	22.35	0.3	91.0	0.1	8.6	0.4	99.6	1

the sense that its relative increase in number of individuals is much greater. The point is readily documented by averaging together for the I, II, and III volumes those percentages listed in the appropriate tables for each of the three series (E-a, E-b, and E-c) at the 90-day census. These averages are as follows:

	T. castaneum %	*T. confusum* %
E-a	80.0	20.0
E-b	50.9	49.1
E-c	93.4	6.6

Thus, the proportional representation of *T. confusum* in E-a, E-b, and E-c is, respectively, 30.0, 25.9, and 18.4% *less* than would be expected on the assumption that, individual for individual, both species are evenly matched during this period of establishment. This interesting fact has no common relation to species *extinction*, however, for, as we have already seen, it is *T. castaneum* that eventually dies in all these 66 populations now under review. The major point reaffirmed here is that it *is* possible for *T. castaneum* to reproduce effectively in the presence of *T. confusum*.

The remarks above serve as a description of the early phase of growth of the E-b cultures. The period of decline for *T. castaneum* illustrated in Figure 10 should now be examined. This takes place, as it

did for the E-a series, in all three volumes. The decline is of less magnitude because the maximal densities at day-90 were lower. But it is appreciable nevertheless and, occurring as it does over the same time interval, re-enforces the conclusion that it is caused primarily by an increasing infection pressure exerted by Adelina. This contraction of the *T. castaneum* component of the various experimental populations leads to the complete extinction of this species. By day-360, the two III-E-b cultures have become controls; the last I-E-b replicate is gone at day-750; and the last II-E-b, at day-540. The median extinction ages are 360, 360, and 345 days for volumes I, II, and III, respectively.

I-E-c, II-E-c, and III-E-c populations.—The performances of these three sets of experimental popu-

TABLE 18. I-E-b: *Tribolium castaneum* becoming extinct.

Age (days)	Mean Number Per Gram									Percentage of						n
	T. castaneum			*T. confusum*			Total			Larvae and Pupae		Imagoes		Total		
	L-P	Imag.	Sum	L-P	Imag.	Sum	L-P	Imag.	Sum	*T. cast.*	*T. conf.*	*T. cast.*	*T. conf.*	*T. cast.*	*T. conf.*	
30.......	5.8	1.1	6.9	15.0	1.0	16.0	20.8	2.1	22.9	25.3	65.5	4.8	4.4	30.1	69.9	15
60.......	3.1	5.1	8.2	2.2	10.3	12.5	5.3	15.4	20.7	15.0	10.6	24.6	49.8	39.6	60.4	15
90.......	5.3	5.1	10.4	1.1	10.1	11.2	6.4	15.2	21.6	24.5	5.1	23.7	46.7	48.2	51.8	15
120.......	3.5	4.1	7.6	0.7	9.8	10.5	4.2	13.9	18.1	19.3	3.9	22.7	54.1	42.0	58.0	15
150.......	4.3	3.6	7.9	0.9	9.2	10.1	5.2	12.8	18.0	23.9	5.0	20.0	51.1	43.9	56.1	15
180.......	4.1	3.0	7.1	1.5	8.5	10.0	5.6	11.5	17.1	24.0	8.8	17.5	49.7	41.5	58.5	15
210.......	2.7	2.0	4.7	1.6	7.6	9.2	4.3	9.6	13.9	19.4	11.5	14.4	54.7	33.8	66.2	15
240.......	2.6	1.5	4.1	2.8	6.6	9.4	5.4	8.1	13.5	19.3	20.7	11.1	48.9	30.4	69.6	15
270.......	3.3	1.1	4.4	4.2	6.4	10.6	7.5	7.5	15.0	22.0	28.0	7.3	42.7	29.3	70.7	14
300.......	3.7	0.9	4.6	5.5	6.2	11.7	9.2	7.1	16.3	22.7	33.7	5.5	38.1	28.2	71.8	11
330.......	2.9	0.8	3.7	4.9	6.7	11.6	7.8	7.5	15.3	18.9	32.0	5.3	43.8	24.2	75.8	10
360.......	1.4	0.8	2.2	5.0	6.3	11.3	6.4	7.1	13.5	10.4	37.0	5.9	46.7	16.3	83.7	7
390.......	3.1	0.9	4.0	6.0	5.1	11.1	9.1	6.0	15.1	20.5	39.7	6.0	33.8	26.5	73.5	5
420.......	2.1	0.6	2.7	6.6	5.8	12.4	8.7	6.4	15.1	13.9	43.7	4.0	38.4	17.9	82.1	5
450.......	2.4	0.7	3.1	7.8	5.9	13.7	10.2	6.6	16.8	14.3	46.4	4.2	35.1	18.5	81.5	4
480.......	1.2	0.5	1.7	6.5	7.2	13.7	7.7	7.7	15.4	7.8	42.2	3.2	46.8	11.0	89.0	4
510.......	1.2	0.4	1.6	7.4	8.0	15.4	8.6	8.4	17.0	7.1	43.5	2.3	47.1	9.4	90.6	4
540.......	0.6	0.3	0.9	8.9	8.6	17.5	9.5	8.9	18.4	3.3	48.4	1.6	46.7	4.9	95.1	4
570.......	0.4	0.2	0.6	7.8	9.3	17.1	8.2	9.5	17.7	2.3	44.1	1.1	52.5	3.4	96.6	4
600.......	0.3	0.2	0.5	4.8	10.4	15.2	5.1	10.6	15.7	1.9	30.6	1.3	66.2	3.2	96.8	3
630.......	0.2	0.1	0.3	6.8	10.3	17.1	7.0	10.4	17.4	1.1	39.1	0.6	59.2	1.7	98.3	2
660.......	0.2	0.1	0.3	7.0	9.1	16.1	7.2	9.2	16.4	1.2	42.7	0.6	55.5	1.8	98.2	2
690.......	0.3	0.1	0.4	11.6	8.6	20.2	11.9	8.7	20.6	1.5	56.3	0.4	41.8	1.9	98.1	2
720.......	0.2	0.1	0.3	10.2	11.6	21.8	10.4	11.7	22.1	0.9	46.1	0.5	52.5	1.4	98.6	1

TABLE 19. II-E-b: *Tribolium castaneum* becoming extinct.

Age (days)	Mean Number Per Gram									Percentage of						n
	T. castaneum			*T. confusum*			Total			Larvae and Pupae		Imagoes		Total		
	L-P	Imag.	Sum	L-P	Imag.	Sum	L-P	Imag.	Sum	*T. cast.*	*T. conf.*	*T. cast.*	*T. conf.*	*T. cast.*	*T. conf.*	
30.......	2.8	2.6	5.4	13.0	2.5	15.5	15.8	5.1	20.9	13.4	62.2	12.4	12.0	25.8	74.2	7
60.......	3.6	6.0	9.6	2.1	9.6	11.7	5.7	15.6	21.3	16.9	9.9	28.2	45.0	45.1	54.9	7
90.......	5.8	5.8	11.6	1.0	9.4	10.4	6.8	15.2	22.0	26.4	4.5	26.3	42.8	52.7	47.3	7
120.......	4.7	4.7	9.4	0.6	9.2	9.8	5.3	13.9	19.2	24.5	3.1	24.5	47.9	49.0	51.0	7
150.......	4.7	3.8	8.5	0.6	8.4	9.0	5.3	12.2	17.5	26.9	3.4	21.7	48.0	48.6	51.4	7
180.......	4.0	2.8	6.8	1.0	7.4	8.4	5.0	10.2	15.2	26.3	6.6	18.4	48.7	44.7	55.3	7
210.......	4.3	2.7	7.0	1.8	6.4	8.2	6.1	9.1	15.2	28.3	11.8	17.8	42.1	46.1	53.9	7
240.......	3.8	0.7	4.5	3.0	6.1	9.1	6.8	6.8	13.6	27.9	22.1	5.2	44.8	33.1	66.9	7
270.......	3.5	1.0	4.5	3.5	7.2	10.7	7.0	8.2	15.2	23.0	23.0	6.6	47.4	29.6	70.4	7
300.......	0.6	0.1	0.7	6.9	7.8	14.7	7.5	7.9	15.4	3.9	44.8	0.7	50.6	4.6	95.4	6
330.......	0.31	0.09	0.40	6.45	8.38	14.83	6.76	8.47	15.23	2.0	42.4	0.6	55.0	2.6	97.4	4
360.......	0.19	0.08	0.27	4.88	7.49	12.37	5.07	7.57	12.64	1.5	38.6	0.6	59.3	2.1	97.9	3
390.......	0.31	0.07	0.38	6.43	6.52	12.95	6.74	6.59	13.33	2.3	48.2	0.6	48.9	2.9	97.1	3
420.......	0.27	0.08	0.35	9.08	7.02	16.10	9.35	7.10	16.45	1.6	55.2	0.5	42.7	2.1	97.9	2
450.......	0.19	0.05	0.24	9.69	7.55	17.24	9.88	7.60	17.48	1.1	55.4	0.3	43.2	1.4	98.6	1
480.......	0.13	0.03	0.16	9.30	7.12	16.42	9.43	7.15	16.58	0.8	56.1	0.2	42.9	1.0	99.0	1
510.......	0.23	0.05	0.28	11.04	5.80	16.84	11.27	5.85	17.12	1.3	64.5	0.3	33.9	1.6	98.4	1

lations are recorded in Tables 21, 22, and 23 and graphed in Figure 11. The salient facts can be quickly summarized in the following five points:

(1) The three curves exhibit a general agreement between themselves and a general dissimilarity during the first year to those already discussed.

(2) Once again, the maximum percentage of *T. castaneum* is reached at day-90 at which time *T. confusum* constitutes 9.2 per cent of the total in the I volumes, 6.1% in the II volumes, and 4.5% in the III volumes. As suggested earlier, this very high proportion of *T. castaneum,* higher than that attained in any of the other cultures, is related to the fact that this beetle was introduced initially with a 50% advantage over its competitor plus the added and significant fact that, during this interval, it was able to multiply effectively.

(3) The decline in *T. castaneum,* starting about the time of the fourth or fifth census and so characteristic of E-a and E-b, is equally well displayed by the E-c populations. Actually, this decline is more dramatic for the last group because *T. castaneum* has a greater potentiality for contraction by virtue of its greater early abundance. The period of contraction is similar to that seen in the controls and the other two experimental series—a datum further incriminating Adelina as a causal agent.

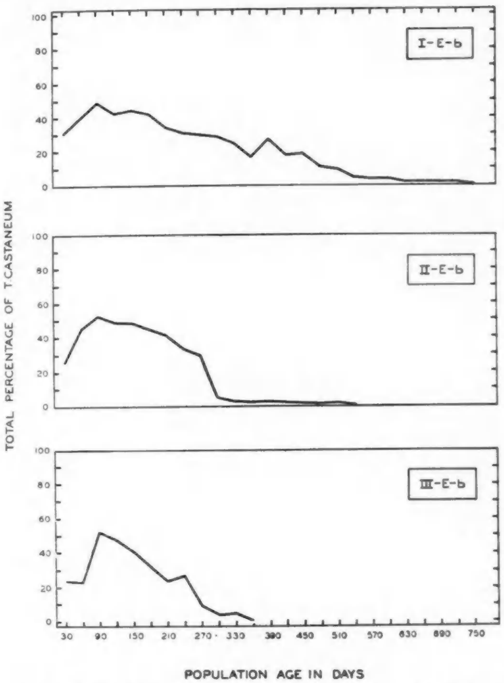

FIG. 10. Competition curves for I-E-b, II-E-b, and III-E-b populations in which *T. castaneum* becomes extinct.

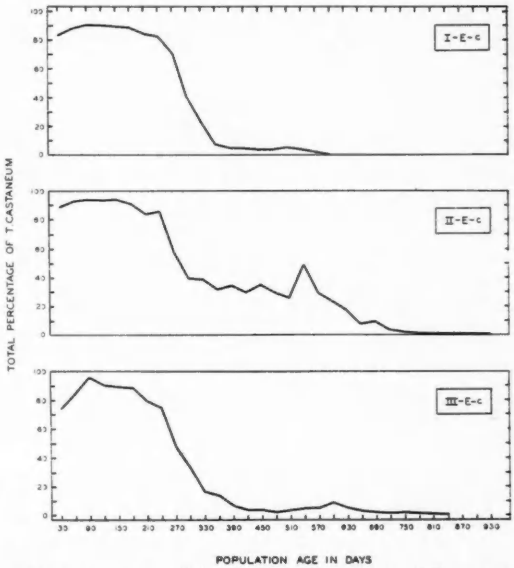

FIG. 11. Competition curves for I-E-c, II-E-c, and III-E-c populations in which *T. castaneum* becomes extinct.

TABLE 20. III-E-b: *Tribolium castaneum* becoming extinct.

Age (days)	Mean Number Per Gram									Percentage of						n
	T. castaneum			*T. confusum*			Total			Larvae and Pupae		Imagoes		Total		
	L-P	Imag.	Sum	L-P	Imag.	Sum	L-P	Imag.	Sum	*T. cast.*	*T. conf.*	*T. cast.*	*T. conf.*	*T. cast.*	*T. conf.*	
30	3.2	1.8	5.0	15.1	1.6	16.7	18.3	3.4	21.7	14.7	69.6	8.4	7.3	23.1	76.9	2
60	2.1	1.7	3.8	2.9	10.0	12.9	5.0	11.7	16.7	12.6	17.4	10.2	59.8	22.8	77.2	2
90	6.2	5.0	11.2	0.5	9.9	10.4	6.7	14.9	21.6	28.7	2.3	23.2	45.8	51.9	48.1	2
120	4.5	4.4	8.9	0.4	9.6	10.0	4.9	14.0	18.9	23.8	2.1	23.3	50.8	47.1	52.9	2
150	2.9	3.5	6.4	0.4	9.1	9.5	3.3	12.6	15.9	18.2	2.5	22.1	57.2	40.3	59.7	2
180	2.4	2.1	4.5	1.5	8.1	9.6	3.9	10.2	14.1	17.0	10.6	14.9	57.5	31.9	68.1	2
210	2.0	0.9	2.9	3.1	6.2	9.3	5.1	7.1	12.2	16.4	25.4	7.4	50.8	23.8	76.2	2
240	2.8	0.4	3.2	4.2	4.5	8.7	7.0	4.9	11.9	23.5	35.3	3.4	37.8	26.9	73.1	2
270	1.2	0.2	1.4	7.9	6.6	14.5	9.1	6.8	15.9	7.5	49.7	1.3	41.5	8.8	91.2	2
300	0.34	0.08	0.42	3.74	7.67	11.41	4.08	7.75	11.83	2.9	31.6	0.7	64.8	3.6	96.4	2
330	0.56	0.01	0.57	5.91	5.90	11.81	6.47	5.91	12.38	4.5	47.7	0.1	47.7	4.6	95.4	1

TABLE 21. I-E-c: *Tribolium castaneum* becoming extinct.

Age (days)	Mean Number Per Gram									Percentage of						n
	T. castaneum			*T. confusum*			Total			Larvae and Pupae		Imagoes		Total		
	L-P	Imag.	Sum	L-P	Imag.	Sum	L-P	Imag.	Sum	*T. cast.*	*T. conf.*	*T. cast.*	*T. conf.*	*T. cast.*	*T. conf.*	
30	14.8	5.9	20.7	3.6	0.5	4.1	18.4	6.4	24.8	59.7	14.5	23.8	2.0	83.5	16.5	11
60	6.7	15.0	21.7	0.4	2.4	2.8	7.1	17.4	24.5	27.3	1.6	61.3	9.8	88.6	11.4	11
90	8.5	15.2	23.7	0.2	2.2	2.4	8.7	17.4	26.1	32.6	0.8	58.2	8.4	90.8	9.2	11
120	7.6	13.6	21.2	0.1	2.2	2.3	7.7	15.8	23.5	32.3	0.4	57.9	9.4	90.2	9.8	11
150	7.7	10.7	18.4	0.1	2.0	2.1	7.8	12.7	20.5	37.6	0.5	52.2	9.7	89.8	10.2	11
180	6.4	7.9	14.3	0.1	1.7	1.8	6.5	9.6	16.1	39.7	0.6	49.1	10.6	88.8	11.2	11
210	5.6	5.0	10.6	0.4	1.6	2.0	6.0	6.6	12.6	44.4	3.2	39.7	12.7	84.1	15.9	11
240	7.2	2.9	10.1	0.8	1.4	2.2	8.0	4.3	12.3	58.8	6.5	23.3	11.4	82.1	17.9	11
270	6.2	1.4	7.6	1.6	1.6	3.2	7.8	3.0	10.8	57.4	14.8	13.0	14.8	70.4	29.6	11
300	3.7	0.8	4.5	3.2	3.3	6.5	6.9	4.1	11.0	33.6	29.1	7.3	30.0	40.9	59.1	11
330	2.6	0.6	3.2	5.1	5.7	10.8	7.7	6.3	14.0	18.6	36.4	4.3	40.7	22.9	77.1	9
360	0.7	0.4	1.1	6.7	7.9	14.6	7.4	8.3	15.7	4.5	42.7	2.5	50.3	7.0	93.0	8
390	0.5	0.2	0.7	6.5	8.5	15.0	7.0	8.7	15.7	3.2	41.4	1.3	54.1	4.5	95.5	5
420	0.5	0.2	0.7	7.1	8.5	15.6	7.6	8.7	16.3	3.1	43.6	1.2	52.1	4.3	95.7	5
450	0.3	0.2	0.5	4.7	8.6	13.3	5.0	8.8	13.8	2.2	34.1	1.4	62.3	3.6	96.4	3
480	0.3	0.2	0.5	5.4	8.1	13.5	5.7	8.3	14.0	2.1	38.6	1.5	57.8	3.6	96.4	3
510	0.5	0.2	0.7	6.1	7.1	13.2	6.6	7.3	13.9	3.6	43.9	1.4	51.1	5.0	95.0	2
540	0.4	0.2	0.6	7.8	7.3	15.1	8.2	7.5	15.7	2.5	49.7	1.3	46.5	3.8	96.2	2
570	0.2	0.1	0.3	9.5	8.4	17.9	9.7	8.5	18.2	1.1	52.2	0.6	46.1	1.7	98.3	2

TABLE 22. II-E-c: *Tribolium castaneum* becoming extinct.

Age (days)	Mean Number Per Gram									Percentage of						n
	T. castaneum			*T. confusum*			Total			Larvae and Pupae		Imagoes		Total		
	L-P	Imag.	Sum	L-P	Imag.	Sum	L-P	Imag.	Sum	*T. cast.*	*T. conf.*	*T. cast.*	*T. conf.*	*T. cast.*	*T. conf.*	
30	13.4	8.0	21.4	2.4	0.3	2.7	15.8	8.3	24.1	55.6	10.0	33.2	1.2	88.8	11.2	7
60	8.5	17.1	25.6	0.3	1.8	2.1	8.8	18.9	27.7	30.7	1.1	61.7	6.5	92.4	7.6	7
90	11.3	16.3	27.6	0.1	1.7	1.8	11.4	18.0	29.4	38.4	0.3	55.5	5.8	93.9	6.1	7
120	7.5	15.3	22.8	0.1	1.6	1.7	7.6	16.9	24.5	30.6	0.4	62.5	6.5	93.1	6.9	7
150	7.7	11.8	19.5	0.1	1.3	1.4	7.8	13.1	20.9	36.8	0.5	56.5	6.2	93.3	6.7	7
180	5.3	7.9	13.2	0.1	1.3	1.4	5.4	9.2	14.6	36.3	0.7	54.1	8.9	90.4	9.6	7
210	3.7	3.7	7.4	0.3	1.2	1.5	4.0	4.9	8.9	41.6	3.4	41.6	13.4	83.2	16.8	7
240	7.9	2.3	10.2	0.5	1.3	1.8	8.4	3.6	12.0	65.8	4.2	19.2	10.8	85.0	15.0	7
270	4.1	0.8	4.9	1.5	2.2	3.7	5.6	3.0	8.6	47.7	17.4	9.3	25.6	57.0	43.0	7
300	3.6	0.7	4.3	2.8	3.9	6.7	6.4	4.6	11.0	32.7	25.4	6.4	35.5	39.1	60.9	7
330	4.2	1.1	5.3	3.7	4.9	8.6	7.9	6.0	13.9	30.2	26.6	7.9	35.3	38.1	61.9	7
360	2.6	1.2	3.8	2.8	5.6	8.4	5.4	6.8	12.2	21.3	22.9	9.9	45.9	31.2	68.8	6
390	3.6	1.2	4.8	4.4	4.9	9.3	8.0	6.1	14.1	25.5	31.2	8.5	34.8	34.0	66.0	5
420	2.6	0.9	3.5	3.8	4.6	8.4	6.4	5.5	11.9	21.8	31.9	7.6	38.7	29.4	70.6	5
450	4.1	0.8	4.9	5.5	3.8	9.3	9.6	4.6	14.2	28.9	38.7	5.6	26.8	34.5	65.5	4
480	2.0	0.8	2.8	3.0	3.7	6.7	5.0	4.5	9.5	21.0	31.6	8.5	38.9	29.5	70.5	3
510	2.0	0.7	2.7	3.9	3.9	7.8	5.9	4.6	10.5	19.0	37.1	6.7	37.2	25.7	74.3	3
540	4.0	0.8	4.8	4.0	2.1	6.1	8.0	2.9	10.9	36.7	36.7	7.3	19.3	44.0	56.0	2
570	2.0	0.8	2.8	3.4	3.3	6.7	5.4	4.1	9.5	21.0	35.8	8.5	34.7	29.5	70.5	2
600	2.0	0.6	2.6	4.0	4.4	8.4	6.0	5.0	11.0	18.2	36.4	5.4	40.0	23.6	76.4	2
630	1.3	0.5	1.8	3.6	4.9	8.5	4.9	5.4	10.3	12.6	34.9	4.9	47.6	17.5	82.5	2
660	0.5	0.3	0.8	4.1	5.5	9.6	4.6	5.8	10.4	4.8	39.4	2.9	52.9	7.7	92.3	2
690	0.9	0.3	1.2	5.6	5.8	11.4	6.5	6.1	12.6	7.1	44.4	2.4	46.1	9.5	90.5	2
720	0.3	0.2	0.5	6.1	8.3	14.4	6.4	8.5	14.9	2.0	40.9	1.4	55.7	3.4	96.6	2
750	0.1	0.1	0.2	2.1	9.0	11.1	2.2	9.1	11.3	0.9	18.6	0.9	79.6	1.8	98.2	2
780	0.06	0.05	0.11	3.47	9.12	12.59	3.53	9.17	12.70	0.5	27.3	0.4	71.8	0.9	99.1	1
810	0.08	0.05	0.13	5.93	8.22	14.15	6.01	8.27	14.28	0.6	41.5	0.3	57.6	0.9	99.1	1
840	0.03	0.05	0.08	5.44	9.48	14.92	5.47	9.53	15.00	0.2	36.3	0.3	63.2	0.5	99.5	1
870	0.09	0.05	0.14	6.82	8.32	15.14	6.91	8.37	15.28	0.6	44.6	0.3	54.5	0.9	99.1	1
900	0.10	0.02	0.12	11.23	8.00	19.23	11.33	8.02	19.35	0.5	58.0	0.1	41.4	0.6	99.4	1

TABLE 23. III-E-c: *Tribolium castaneum* becoming extinct.

Age (days)	MEAN NUMBER PER GRAM									PERCENTAGE OF						n
	T. castaneum			*T. confusum*			Total			Larvae and Pupae		Imagoes		Total		
	L-P	Imag.	Sum	L-P	Imag.	Sum	L-P	Imag.	Sum	*T. cast.*	*T. conf.*	*T. cast.*	*T. conf.*	*T. cast.*	*T. conf.*	
30	11.4	5.5	16.9	5.5	0.5	6.0	16.9	6.0	22.9	49.8	24.0	24.0	2.2	73.8	26.2	2
60	6.3	13.6	19.9	2.0	1.8	3.8	8.3	15.4	23.7	26.6	8.4	57.4	7.6	84.0	16.0	2
90	12.3	11.2	23.5	0.1	1.0	1.1	12.4	12.2	24.6	50.0	0.4	45.5	4.1	95.5	4.5	2
120	9.8	12.5	22.3	0.1	2.3	2.4	9.9	14.8	24.7	39.7	0.4	50.6	9.3	90.3	9.7	2
150	6.3	10.2	16.5	0.1	1.9	2.0	6.4	12.1	18.5	34.0	0.5	55.2	10.3	89.2	10.8	2
180	7.5	6.8	14.3	0.3	1.5	1.8	7.8	8.3	16.1	46.6	1.9	42.2	9.3	88.8	11.2	2
210	4.5	2.7	7.2	0.5	1.4	1.9	5.0	4.1	9.1	49.4	5.5	29.7	15.4	79.1	20.9	2
240	5.8	1.2	7.0	0.9	1.5	2.4	6.7	2.7	9.4	61.7	9.6	12.8	15.9	74.5	25.5	2
270	4.6	0.6	5.2	3.5	2.2	5.7	8.1	2.8	10.9	42.2	32.1	5.5	20.2	47.7	52.3	2
300	4.3	0.5	4.8	4.6	5.0	9.6	8.9	5.5	14.4	29.9	31.9	3.4	34.8	33.3	66.7	2
330	1.8	0.4	2.2	4.8	6.4	11.2	6.6	6.8	13.4	13.4	35.8	3.0	47.8	16.4	83.6	2
360	1.1	0.4	1.5	3.3	6.6	9.9	4.4	7.0	11.4	9.6	28.9	3.6	57.9	13.2	86.8	2
390	0.6	0.2	0.8	5.5	6.3	11.8	6.1	6.5	12.6	4.8	43.6	1.6	50.0	6.4	93.6	2
420	0.4	0.1	0.5	7.6	6.2	13.8	8.0	6.3	14.3	2.8	53.1	0.7	43.4	3.5	96.5	2
450	0.49	0.09	0.58	9.55	6.76	16.31	10.04	6.85	16.89	2.9	32.9	0.5	63.7	3.4	96.6	2
480	0.20	0.07	0.27	6.56	6.64	13.20	6.76	6.71	13.47	1.5	48.7	0.5	49.3	2.0	98.0	2
510	0.45	0.08	0.53	10.62	6.04	16.66	11.07	6.12	17.19	2.6	61.8	0.5	35.1	3.1	96.9	2
540	0.5	0.2	0.7	7.7	7.4	15.1	8.2	7.6	15.8	3.2	48.7	1.2	46.9	4.4	95.6	2
570	0.4	0.2	0.6	5.6	6.9	12.5	6.0	7.1	13.1	3.0	42.7	1.6	52.7	4.6	95.4	2
600	0.9	0.2	1.1	6.3	6.1	12.4	7.2	6.3	13.5	6.7	46.7	1.5	45.1	8.2	91.8	2
630	0.6	0.1	0.7	9.6	5.6	15.2	10.2	5.7	15.9	3.8	60.4	0.6	35.2	4.4	95.6	2
660	0.28	0.09	0.37	8.08	6.16	14.24	8.36	6.25	14.61	1.9	55.3	0.6	42.2	2.5	97.5	2
690	0.26	0.06	0.32	11.22	5.64	16.86	11.48	5.70	17.18	1.5	65.3	0.4	32.8	1.9	98.1	2
720	0.21	0.05	0.26	12.90	6.64	19.54	13.11	6.69	19.80	1.1	65.1	0.2	33.6	1.3	98.7	2
750	0.27	0.05	0.32	16.00	5.49	21.49	16.27	5.54	21.81	1.2	73.4	0.3	25.1	1.5	98.5	1
780	0.11	0.02	0.13	12.44	7.42	19.86	12.55	7.44	19.99	0.5	62.2	0.2	37.1	0.7	99.3	1

(4) There is close confluence between the curves for I-E-c and III-E-c from day-240 until species extinction occurs. The percentage of *T. castaneum* in the II-E-c populations is higher for a number of census readings subsequent to day-270 and certain replicates persist as mixed-species cultures for quite a period.

(5) The temporal relations of extinction for the three experimental series are as follows:

	First extinction (days)	*Median (days)*	*Last survivor (days)*
I-E-c	330	390	600
II-E-c	360	480	930
III-E-c	750	780	810

General conclusions.—In summarizing this section devoted to the extinction of *T. castaneum* when in competition with *T. confusum*, it should be kept in mind that, while the former species characteristically dies out in the presence of the latter, there are exceptions which must be carefully examined in their own right. Such examination follows shortly. Our present responsibility is to discuss the extinction of *T. castaneum* and to offer certain broad suggestions as to how this may come about. These suggestions, advanced as first approximations only, must remain just that pending further research of a more analytical character. As pointed out earlier, the present study, despite its duration and scope, is essentially a *description* of events within populations established in several ways and as such makes no pretense at being anything like a final interpretation of these events. All interpretations in this paper, therefore, are to be regarded as exploratory and suggestive rather than as definitive.

Consideration of the following topics affords a brief summary of this section: (1) ages at which *T. castaneum* becomes extinct within and between the several experimental series; (2) increase of *T. castaneum* during the first ninety days of observation; (3) decrease of *T. castaneum* during the interval from day-90 to day-360 or thereabouts; (4) the final dying out of this species and conversion of the cultures to control populations of *T. confusum;* and (5) the rôle of parasitic infection and interspecies competition in the extinction process.

(1) It is possible to draw certain further conclusions regarding the time of extinction of *T. castaneum* from the data contained in Table 14. Since only two replicates exist for each of the three series III cultures, no statistical analysis is permissible. Something can be attempted for series I and II, however, despite the unavoidable fact that the numbers are admittedly inadequate. Mean ages at extinction have been compared between and within volumes, making use of a variant of Student's small-sample method that allows comparison of unpaired data for which the N is low. This method has been applied to the following mean differences, the appropriate probabilities being indicated within the parentheses:

I-E-a minus I-E-b	(24%)
I-E-a minus I-E-c	(21%)
I-E-c minus I-E-b	(>50%)
II-E-a minus II-E-b	(22%)
II-E-c minus II-E-a	(>50%)
II-E-c minus II-E-b	(8%)
II-E-a minus I-E-a	(>50%)
I-E-b minus II-E-b	(49%)
II-E-c minus I-E-c	(13%)

From the above tabulation it is clear that no statistically significant differences exist between these figures. Differently put, and remembering the limitations imposed by the small size of the samples, no differential in mean survival time of *T. castaneum* populations in competition with *T. confusum* is demonstrated for series I and II. This holds true irrespective of the volume and of the initial ratios between the two species established when the experimentals were first started.

In some respects the median is a better index of survival time than is the mean because it is not so influenced by the long persistence of certain cultures as mixed-species populations and because most of the distributions are skewed, usually in a positive direction. Calculation of the significance of the difference between the various medians showed that only those comparisons of I-E-a with I-E-b and I-E-a with I-E-c exhibited a probability lower than one per cent, 210 ± 50.5 days and 180 ± 44.9 days, respectively. All other differences were in excess of the five per cent point.

(2) The preceding discussion has established the fact that *T. castaneum* increases disproportionately (relative to its associate) during the first ninety days irrespective of initial density. During this period the percentage of *T. confusum* is declining. This relationship holds even for the E-b populations in which *T. castaneum* is in competition with a large number of beetles of the other species, and it leads to the suggestion that the former species can multiply effectively when in association with *T. confusum*. At least three points can be advanced in explanation of this: (a) the higher reproductive potential of *T. castaneum;* (b) the slightly faster rate of development of this species; and (c) the fact that *T. castaneum* is not heavily infected with Adelina during these three months in consequence of which its rate of mortality is low. Of course, *T. confusum* also exerts some competitive effect upon *T. castaneum*, as is suggested perhaps by the observation that the experimental cultures do not attain as great densities of *T. castaneum* as those reported for comparable controls. This aspect of competition, however, is outweighed through the operation of the three factors enumerated above.

(3) All the experimental populations described up to this point are characterized by a drop in percentage of *T. castaneum* which is first seen at the fourth census. Were this decline, which typically reaches its nadir around day-360, confined to the mixed-species cultures, it could reasonably be assumed that the cause lay in competitive pressures directed against *T. castaneum* and established through the activities of the *T. confusum* populations. Something of this probably obtains for the latter species becomes increasingly more abundant as the first species contracts. But, since this reduction of *T. castaneum* is so characteristic of control populations when Adelina is present and since it essentially disappears when the parasite is removed, it seems clear that infection pressure *per se* is the primary cause.

(4) The final period during which *T. castaneum* actually becomes extinct can be visualized as setting in subsequent to the 300-360 day interval after this species has been reduced by parasitic infection. As we have seen (Table 14) extinction occurs soon thereafter for certain individual populations but it may be quite postponed for others. In one previously discussed case (III-E-a) a rather striking "rejuvenation" of *T. castaneum* occurred that resulted in an extended period of semi-equilibrium between the two species although even here the eventual outcome was the death of this form. Characteristically, the percentage of *T. castaneum* is low (usually well under 5% of the total) during the 90-150 days prior to extinction, although exceptions occur notably among the III-E-b replicates. This implies that the populations are not effectively reproducing during the end-period but surviving only until the last deaths take place. As the experimental cultures become single-species populations, equilibria, similar to those of the controls at the same ages, are established. Data supporting this are presented later in Table 28.

(5) Up to this point, our interest has centered on the extinction of *T. castaneum* when in competition with *T. confusum*. This, as has been described, is by far the most usual consequence of such competition in the sense that it happens much more frequently than would be expected purely on the basis of chance. Because the analysis has not yet gone far enough, a definitive explanation of the phenomenon cannot be advanced at this time. It is permissible, however, to order the known facts in a logically consistent pattern, this to be followed by broad generalizations of interpretative value. Two significant points have been established: (a) that *T. castaneum*, when not heavily parasitized, can multiply in association with *T. confusum*, and (b) that, as infection pressure mounts, the *T. castaneum* component of the ecosystem is reduced in much the same way as seen in the control or single species cultures. This leads to the conception that, after something like a year of existence in mixed-species populations, *T. castaneum* attains such low densities not primarily because of *T. confusum* but rather because of Adelina.

At this time the populations of *T. castaneum* are uniformly small, there is presumably a large reservoir of infection, and the relatively abundant *T. confusum*, in numerical terms at least, is the flourishing species. It is a reasonable supposition that these situations, operating together, are sufficient to cause the continuation of that observed decline of *T. castaneum* which leads to its eventual extinction. This view presupposes that *T. confusum* does exert some

adverse effects upon its associate—effects especially important at this stage in the populations' life-history when *T. castaneum* is both sparse and stoutly infected and therefore highly vulnerable. The nature of this adverse competition is not identified, of course, by merely concluding that it exists, and the matter must be left in this state for the present time.

Earlier it was indicated that, for selected populations of I-E-a and I-E-c, *T. confusum* dies out instead of *T. castaneum*. This shows immediately that the events just outlined do not invariably occur in the combination and intensity required to drive out beetles of the latter species and logically introduces the next section devoted to this segment of the study.

EXTINCTION CURVES FOR T. CASTANEUM AND T. CONFUSUM COMPARED

Excluding the sterile, mixed-species cultures (I-E-a-S) shortly to be discussed, the extinction of *T. confusum* when competing with *T. castaneum* is an unusual event limited to eight series I replicates out of a total of 45. Four of these extinctions occur in I-E-a and four in I-E-c and these, as exceptions to the general rule, merit brief discussion. In passing, it is interesting to note that the I-E-b populations, started with a preponderance of *T. confusum* imagoes, and the series II and III cultures which together comprise a sample of 44, all wind up eventually as control populations of *T. confusum*.

Tables 15, 21, 24, and 25 deal with these two sets of I-E-a and I-E-c populations, and the appropriate competition curves are graphed in Figures 9, 11, and 12.

For convenience, those populations in which *T. castaneum* dies out will be referred to as "c-extinct" and those in which the opposite occurs as "b-extinct."

When the curves describing the extinction of *T. castaneum* (Figures 9 and 11) are compared with those for the extinction of *T. confusum* (Figure 12) dissimilarities are immediately evident.

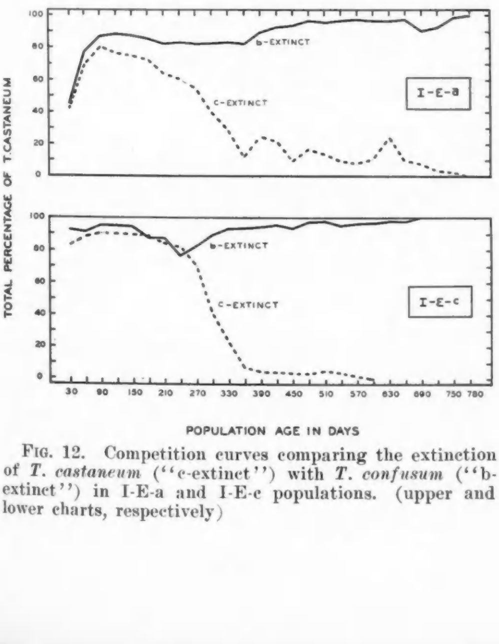

FIG. 12. Competition curves comparing the extinction of *T. castaneum* ("c-extinct") with *T. confusum* ("b-extinct") in I-E-a and I-E-c populations. (upper and lower charts, respectively)

The I-E-a, b-extinct cultures build up larger total populations of *T. castaneum* during the early period of growth than does the c-extinct group. This is true both in terms of percentages and actual numbers per gram. The percentage curves never intercross. For example, at day-90, 80.2% is *T. castaneum* in the one set of replicates (c-extinct) while 87.2% is *T. castaneum* in the other set (b-extinct). Comparable percentages for several succeeding censuses are as follows:

Age (days)	*(c-extinct)*	*(b-extinct)*
120	76.3	88.6
150	74.9	87.6
180	72.0	85.8
210	63.6	82.4
240	60.6	83.1

Expressed as actual numbers, there is, again no intercrossing between the two groups except at day-90. *T. castaneum* does exhibit its characteristic decline induced by Adelina, but this is not as marked for the b-extinct as it is for the c-extinct cultures.

Associated with these higher densities of *T. castaneum* are correspondingly lower densities of *T. confusum*. Apparently, the latter species, in the face of this increased competition, does not become as well established as in the other I-E-a populations (i.e., c-extinct). By the time *T. castenum* has passed through its major "infection crisis" in the b-extinct sample and has started to increase again as happens at day-360, *T. confusum* has undergone further reduction, is not able to control its now more sturdy associate, and, in consequence, declines gradually, to die out at days 510, 630, 690, and 780, respectively.

Occurrences within the I-E-c, b-extinct cultures are essentially similar to those just described, although not quite as clear-cut because *T. castaneum* reaches densities that are lower than in the c-extinct series at several censuses. There is once more, however, a decided rejuvenation of this species at day-270 strongly reminiscent of events in I-C-c—a rejuvenation not present when the beetle is to die out later.

A further discussion of these matters is best postponed until the sterile populations have been dealt with. With that accomplished, it is possible to attempt a synthesis of the various facts described thus far and to discuss in a general way the question of interspecies competition as it exists within populations of these two species of flour beetles.

EXTINCTION OF T. CASTANEUM AND T. CONFUSUM IN THE ABSENCE OF ADELINA

The data dealing with the sterile, mixed-species cultures are presented in Tables 26 and 27 and graphed in Figure 13. Figure 14 assembles in one place the trends of both *Tribolium confusum* and *Tribolium castaneum* in the four sets of Series I populations (I-E-a, c-extinct; I-E-a, b-extinct; I-E-a-S, c-extinct; and I-E-a-S, b-extinct) and uses an ordinate scale of mean number per gram.

As already mentioned, the most significant qualitative fact which emerges when Adelina is removed is that the typical outcome of competition, so charac-

TABLE 24. I-E-a: *Tribolium confusum* becoming extinct.

Age (days)	Mean Number Per Gram									Percentage of						n
	T. castaneum			*T. confusum*			Total			Larvae and Pupae		Imagoes		Total		
	L-P	Imag.	Sum	L-P	Imag.	Sum	L-P	Imag.	Sum	*T. cast.*	*T. conf.*	*T. cast.*	*T. conf.*	*T. cast.*	*T. conf.*	
30	8.2	1.1	9.3	10.8	0.5	11.3	19.0	1.6	20.6	39.8	52.4	5.3	2.5	45.1	54.9	4
60	6.1	10.4	16.5	1.7	3.0	4.7	7.8	13.4	21.2	28.8	8.0	49.0	14.2	77.8	22.2	4
90	10.5	10.6	21.1	0.3	2.8	3.1	10.8	13.4	24.2	43.4	1.2	43.8	11.6	87.2	12.8	4
120	14.8	10.2	25.0	0.4	2.8	3.2	15.2	13.0	28.2	52.5	1.4	36.1	10.0	88.6	11.4	4
150	8.3	9.4	17.7	0.1	2.4	2.5	8.4	11.8	20.2	41.1	0.5	46.5	11.9	87.6	12.4	4
180	7.0	8.1	15.1	0.3	2.2	2.5	7.3	10.3	17.6	39.8	1.7	46.0	12.5	85.8	14.2	4
210	5.0	5.8	10.8	0.3	2.0	2.3	5.3	7.8	13.1	38.2	2.3	44.2	15.3	82.4	17.6	4
240	7.9	3.9	11.8	0.8	1.6	2.4	8.7	5.5	14.2	55.6	5.6	27.5	11.3	83.1	16.9	4
270	7.9	2.9	10.8	0.8	1.5	2.3	8.7	4.4	13.1	60.3	6.1	22.1	11.5	82.4	17.6	4
300	7.4	2.2	9.6	0.8	1.2	2.0	8.2	3.4	11.6	63.8	6.9	19.0	10.3	82.8	17.2	4
330	5.9	2.0	7.9	0.6	1.0	1.6	6.5	3.0	9.5	62.1	6.3	21.1	10.5	83.2	16.8	4
360	12.1	2.3	14.4	2.1	0.9	3.0	14.2	3.2	17.4	69.5	12.1	13.3	5.1	82.8	17.2	4
390	10.6	3.6	14.2	0.8	0.8	1.6	11.4	4.4	15.8	67.1	5.1	22.8	5.0	89.9	10.1	4
420	9.9	3.7	13.6	0.5	0.6	1.1	10.4	4.3	14.7	67.3	3.4	25.2	4.1	92.5	7.5	4
450	12.9	3.9	16.8	0.6	0.5	1.1	13.5	4.4	17.9	72.1	3.3	21.7	2.9	93.8	6.2	4
480	8.8	4.1	12.9	0.2	0.3	0.5	9.0	4.4	13.4	65.7	1.5	30.6	2.2	96.3	3.7	4
510	10.3	4.1	14.4	0.3	0.4	0.7	10.6	4.5	15.1	68.2	2.0	27.2	2.6	95.4	4.6	3
540	10.9	4.0	14.9	0.3	0.2	0.5	11.2	4.2	15.4	70.8	1.9	25.9	1.4	96.7	3.3	3
570	10.0	3.9	13.9	0.2	0.2	0.4	10.2	4.1	14.3	69.9	1.4	27.3	1.4	97.2	2.8	3
600	10.2	3.3	13.5	0.3	0.2	0.5	10.5	3.5	14.0	72.9	2.1	23.5	1.5	96.4	3.6	3
630	8.8	3.3	12.1	0.2	0.2	0.4	9.0	3.5	12.5	70.4	1.6	26.4	1.6	96.8	3.2	2
660	10.2	3.4	13.6	0.2	0.2	0.4	10.4	3.6	14.0	72.9	1.4	24.2	1.5	97.1	2.9	2
690	17.1	2.5	19.6	0.7	0.2	0.9	17.8	2.7	20.5	83.4	3.4	12.2	1.0	95.6	4.4	1
720	13.3	4.7	18.0	0.3	0.2	0.5	13.6	4.9	18.5	71.9	1.6	25.4	1.1	97.3	2.7	1
750	10.7	4.4	15.1	0.1	0.1	0.2	10.8	4.5	15.3	69.9	0.6	29.0	0.5	98.9	1.1	1

TABLE 25. I-E-e: *Tribolium confusum* becoming extinct.

Age (days)	Mean Number Per Gram									Percentage of						n
	T. castaneum			*T. confusum*			Total			Larvae and Pupae		Imagoes		Total		
	L-P	Imag.	Sum	L-P	Imag.	Sum	L-P	Imag.	Sum	*T. cast.*	*T. conf.*	*T. cast.*	*T. conf.*	*T. cast.*	*T. conf.*	
30	14.2	7.9	22.1	1.5	0.3	1.8	15.7	8.2	23.9	59.4	6.3	33.1	1.2	92.5	7.5	4
60	6.4	15.9	22.3	0.3	1.8	2.1	6.7	17.7	24.4	26.2	1.2	65.2	7.4	91.4	8.6	4
90	8.8	15.9	24.7	0.1	1.1	1.2	8.9	17.0	25.9	34.0	0.4	61.4	4.2	95.4	4.6	4
120	8.5	15.2	23.7	0.1	1.1	1.2	8.6	16.3	24.9	34.1	0.4	61.1	4.4	95.2	4.8	4
150	7.9	12.7	20.6	0.1	1.0	1.1	8.0	13.7	21.7	36.4	0.5	58.5	4.6	94.9	5.1	4
180	3.2	7.0	10.2	0.1	1.3	1.4	3.3	8.3	11.6	27.6	0.9	60.3	11.2	87.9	12.1	3
210	6.1	3.0	9.1	0.2	1.1	1.3	6.3	4.1	10.4	58.6	1.9	28.9	10.6	87.5	12.5	3
240	4.6	1.7	6.3	0.8	1.1	1.9	5.4	2.8	8.2	56.1	9.8	20.7	13.4	76.8	23.2	3
270	9.9	1.5	11.4	1.4	1.0	2.4	11.3	2.5	13.8	71.7	10.1	10.9	7.3	82.6	17.4	3
300	8.7	2.2	10.9	0.6	0.7	1.3	9.3	2.9	12.2	71.3	4.9	18.0	5.8	89.3	10.7	3
330	8.2	2.9	11.1	0.3	0.5	0.8	8.5	3.4	11.9	68.9	2.5	24.5	4.1	93.4	6.6	3
360	9.0	3.0	12.0	0.5	0.3	0.8	9.5	3.3	12.8	70.3	3.9	23.4	2.4	93.7	6.3	3
390	7.3	2.2	9.5	0.3	0.3	0.6	7.6	2.5	10.1	72.3	3.0	21.8	2.9	94.1	5.9	3
420	6.7	1.8	8.5	0.2	0.2	0.4	6.9	2.0	8.9	75.3	2.2	20.2	2.3	95.5	4.5	2
450	9.2	1.4	10.6	0.5	0.2	0.7	9.7	1.6	11.3	81.4	4.4	12.4	1.8	93.8	6.2	2
480	8.9	2.4	11.3	0.2	0.1	0.3	9.1	2.5	11.6	76.7	1.7	20.7	0.9	97.4	2.6	2
510	7.1	1.9	9.0	0.1	0.1	0.2	7.2	2.0	9.2	77.2	1.1	20.6	1.1	97.8	2.2	2
540	2.7	1.1	3.8	0.1	0.1	0.2	2.8	1.2	4.0	67.5	2.5	27.5	2.5	95.0	5.0	1
570	6.2	1.6	7.8	0.2	0.1	0.3	6.4	1.7	8.1	76.5	2.5	19.8	1.2	96.3	3.7	1
600	7.8	1.4	9.2	0.2	0.1	0.3	8.0	1.5	9.5	82.1	2.1	14.7	1.1	96.8	3.2	1
630	7.9	1.9	9.8	0.1	0.1	0.2	8.0	2.0	10.0	79.0	1.0	19.0	1.0	98.0	2.0	1
660	9.7	1.6	11.3	0.2	0.1	0.3	9.9	1.7	11.6	83.6	1.7	13.8	0.9	97.4	2.6	1

TABLE 26. I-E-a-S: *Tribolium castaneum* becoming extinct.

Age (days)	Mean Number Per Gram									Percentage of						n
	T. castaneum			*T. confusum*			Total			Larvae and Pupae		Imagoes		Total		
	L-P	Imag.	Sum	L-P	Imag.	Sum	L-P	Imag.	Sum	*T. cast.*	*T. conf.*	*T. cast.*	*T. conf.*	***T. cast.***	***T. conf.***	
30	3.5	1.7	5.2	16.0	2.2	18.2	19.5	3.9	23.4	15.0	68.4	7.2	9.4	**22.2**	**77.8**	6
60	3.1	4.5	7.6	3.5	13.4	16.9	6.6	17.9	24.5	12.6	14.3	18.4	54.7	**31.0**	**69.0**	6
90	4.0	4.5	8.5	1.0	13.6	14.6	5.0	18.1	23.1	17.3	4.3	19.5	58.9	**36.8**	**63.2**	6
120	6.0	3.9	9.9	0.2	13.1	13.3	6.2	17.0	23.2	25.9	0.9	16.8	56.4	**42.7**	**57.3**	6
150	2.5	3.0	5.5	0.7	12.5	13.2	3.2	15.5	18.7	13.4	3.7	16.0	66.9	**29.4**	**70.6**	6
180	3.3	2.2	5.5	1.4	12.1	13.5	4.7	14.3	19.0	17.4	7.4	11.6	63.6	**29.0**	**71.0**	6
210	2.4	1.3	3.7	2.7	8.6	11.3	5.1	9.9	15.0	16.0	18.0	8.7	57.3	**24.7**	**75.3**	5
240	1.8	0.8	2.6	5.2	7.8	13.0	7.0	8.6	15.6	11.5	33.3	5.2	50.0	**16.7**	**83.3**	5
270	0.4	0.6	1.0	2.8	8.4	11.2	3.2	9.0	12.2	3.3	22.9	4.9	68.9	**8.2**	**91.8**	3
300	0.3	0.3	0.6	7.0	8.4	15.4	7.3	8.7	16.0	1.9	43.7	1.9	52.5	**3.8**	**96.2**	3
330	0.3	0.2	0.5	6.5	10.4	16.9	6.8	10.6	17.4	1.7	37.4	1.2	59.7	**2.9**	**97.1**	3
360	0.2	0.2	0.4	5.4	10.2	15.6	5.6	10.4	16.0	1.2	33.7	1.3	63.8	**2.5**	**97.5**	1
390	0.2	0.1	0.3	12.0	9.1	21.1	12.2	9.2	21.4	0.9	56.1	0.5	42.5	**1.4**	**98.6**	1
420	0.2	0.1	0.3	7.9	12.0	19.9	8.1	12.1	20.2	1.0	39.1	0.5	59.4	**1.5**	**98.5**	1

TABLE 27. I-E-a-S: *Tribolium confusum* becoming extinct.

Age (days)	Mean Number Per Gram									Percentage of						n
	T. castaneum			*T. confusum*			Total			Larvae and Pupae		Imagoes		Total		
	L-P	Imag.	Sum	L-P	Imag.	Sum	L-P	Imag.	Sum	*T. cast.*	*T. conf.*	*T. cast.*	*T. conf.*	***T. cast.***	***T. conf.***	
30	6.1	4.6	10.7	7.6	1.6	9.2	13.7	6.2	19.9	30.6	38.2	23.2	8.0	**53.8**	**46.2**	12
60	6.3	8.3	14.6	1.7	6.0	7.7	8.0	14.3	22.3	28.2	7.6	37.3	26.9	**65.5**	**34.5**	12
90	10.4	8.4	18.8	0.6	6.0	6.6	11.0	14.4	25.4	40.9	2.4	33.1	23.6	**74.0**	**26.0**	12
120	13.5	8.0	21.5	0.9	5.8	6.7	14.4	13.8	28.2	47.9	3.2	28.3	20.6	**76.2**	**23.8**	12
150	10.0	7.3	17.3	0.5	5.5	6.0	10.5	12.8	23.3	42.9	2.1	31.3	23.7	**74.2**	**25.8**	12
180	14.6	6.9	21.5	0.9	5.3	6.2	15.5	12.2	27.7	52.7	3.2	24.9	19.2	**77.6**	**22.4**	12
210	11.8	7.8	19.6	1.2	4.8	6.0	13.0	12.6	25.6	46.1	4.7	30.5	18.7	**76.6**	**23.4**	12
240	14.3	8.7	23.0	2.2	4.4	6.6	16.5	13.1	29.6	48.3	7.4	29.4	14.9	**77.7**	**22.3**	12
270	12.9	9.0	21.9	2.3	4.1	6.4	15.2	13.1	28.3	45.6	8.1	31.8	14.5	**77.4**	**22.6**	12
300	11.2	9.0	20.2	3.0	3.5	6.5	14.2	12.5	26.7	41.9	11.2	33.7	13.2	**75.6**	**24.4**	12
330	13.5	9.7	23.2	2.4	3.0	5.4	15.9	12.7	28.6	47.2	8.4	33.9	10.5	**81.1**	**18.9**	12
360	21.1	11.8	32.9	1.8	2.5	4.3	22.9	14.3	37.2	56.7	4.8	31.7	6.8	**88.4**	**11.6**	12
390	13.1	12.2	25.3	1.2	1.8	3.0	14.3	14.0	28.3	46.3	4.2	43.1	6.4	**89.4**	**10.6**	12
420	18.3	12.7	31.0	0.7	1.5	2.2	19.0	14.2	33.2	55.1	2.1	38.3	4.5	**93.4**	**6.6**	12
450	15.3	14.1	29.4	0.8	1.2	2.0	16.1	15.3	31.4	48.7	2.5	44.9	3.9	**93.6**	**6.4**	12
480	22.7	14.7	37.4	1.0	1.1	2.1	23.7	15.8	39.5	57.5	2.5	37.2	2.8	**94.7**	**5.3**	12
510	25.1	16.6	41.7	0.7	0.9	1.6	25.8	17.5	43.3	58.0	1.6	38.3	2.1	**96.3**	**3.7**	11
540	25.8	22.2	48.0	0.6	0.8	1.4	26.4	23.0	49.4	52.2	1.2	45.0	1.6	**97.2**	**2.8**	10
570	24.8	21.5	46.3	0.3	0.6	0.9	25.1	22.1	47.2	52.5	0.6	45.6	1.3	**98.1**	**1.9**	9
600	21.5	22.0	43.5	0.1	0.4	0.5	21.6	22.4	44.0	48.9	0.2	50.0	0.9	**98.9**	**1.1**	7
630	12.3	16.5	28.8	0.1	0.3	0.4	12.4	16.8	29.2	42.1	0.3	56.5	1.1	**98.6**	**1.4**	7
660	11.0	16.1	27.1	0.2	0.4	0.6	11.2	16.5	27.7	39.7	0.7	58.1	1.5	**97.8**	**2.2**	5
690	10.7	11.8	22.5	0.3	0.3	0.6	11.0	12.1	23.1	46.4	1.3	51.0	1.3	**97.4**	**2.6**	3
720	5.5	7.4	12.9	0.1	0.3	0.4	5.6	7.7	13.3	41.3	0.7	55.7	2.3	**97.0**	**3.0**	3
750	19.0	8.2	27.2	0.2	0.2	0.4	19.2	8.4	27.6	68.8	0.7	29.7	0.8	**98.5**	**1.5**	3
780	17.6	12.8	30.4	0.1	0.2	0.3	17.7	13.0	30.7	57.3	0.3	41.7	0.7	**99.0**	**1.0**	3
810	23.3	13.1	36.4	0.1	0.1	0.2	23.4	13.2	36.6	63.7	0.3	35.7	0.3	**99.4**	**0.6**	1

teristic of infected cultures, is reversed. In other words, *T. castaneum* now wins more often then does *T. confusum*—an event taking place in 12 out of 18 replicates. This suggests immediately that, in the absence of infection, the usual occurrences within the populations may be, and in fact frequently are, markedly altered. The matter cannot be interpreted exclusively on this basis, however, because *T. confusum* does sometimes drive out *T. castaneum* in sterile cultures as just noted.

This section dealing with the non-infected, competition cultures can be logically developed as follows:

(1) I-E-a compared with I-E-a-S; ***T. confusum*** becoming extinct.

(2) I-E-a compared with I-E-a-S; ***T. castaneum*** becoming extinct.

(3) I-E-a-S (b-extinct) compared with I-E-a-S (c-extinct).

(1) *I-E-a compared with I-E-a-S (b-extinct).*—When I-E-a and I-E-a-S populations in which *T. confusum* becomes extinct are contrasted, certain differences are apparent despite the fact that the eventual outcome is similar. These differences require brief discussion. In the first place, the number of *T. confusum* is greater for the sterile than for the infected group during the first year of the cultures' history. This suggests perhaps that removal of

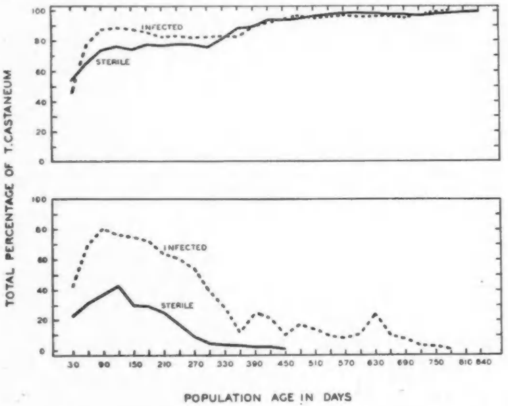

FIG. 13. Competition curves showing the extinction of *T. confusum* (upper chart) and the extinction of *T. castaneum* (lower chart) in I-E-a (marked "infected") and I-E-a-S (marked "sterile") populations.

Adelina has some stimulatory or beneficial effect upon this beetle even though the degree of such stimulation is much less than that seen for *T. castaneum.* The control cultures support this suggestion only to the extent that *T. confusum*, when not parasitized, maintained itself over the total period of observation with a higher percentage of imagoes than it did when parasitized. It is also noteworthy that *T. castaneum* in the sterile series starts its exaggerated growth after day-300 and does not ever exhibit any sign of the depression so very characteristic when Adelina is present and so very important in inducing that decline which, taken in conjunction with competition, results in final extinction. The fact that the numbers of *T. castaneum* are consistently less during the first 150 days for the sterile than for the infected group, also deserves mention. This may well result from an increase in competition pressure caused by the presence of larger populations of *T. confusum* and is supported by the fact that the sterile *controls* of *T. castaneum* (I-C-c-S) are larger than the infected *controls* (I-C-c) even at the first three censuses. Eventually, however, the populations of *T. castaneum* in the sterile cultures become so large that *T. confusum* is completely crowded out. The extinction of *T. confusum* in the I-E-a cultures has already been discussed, and this unusual event was related to the observation that, in these four instances, *T. castaneum* does not attain as low a density for the 270-330 day interval as is usually the case.

(2) *I-E-a compared with I-E-a-S (c-extinct).*—Extinction of *T. castaneum* is the typical end-result of competition in parasitized cultures and the atypical

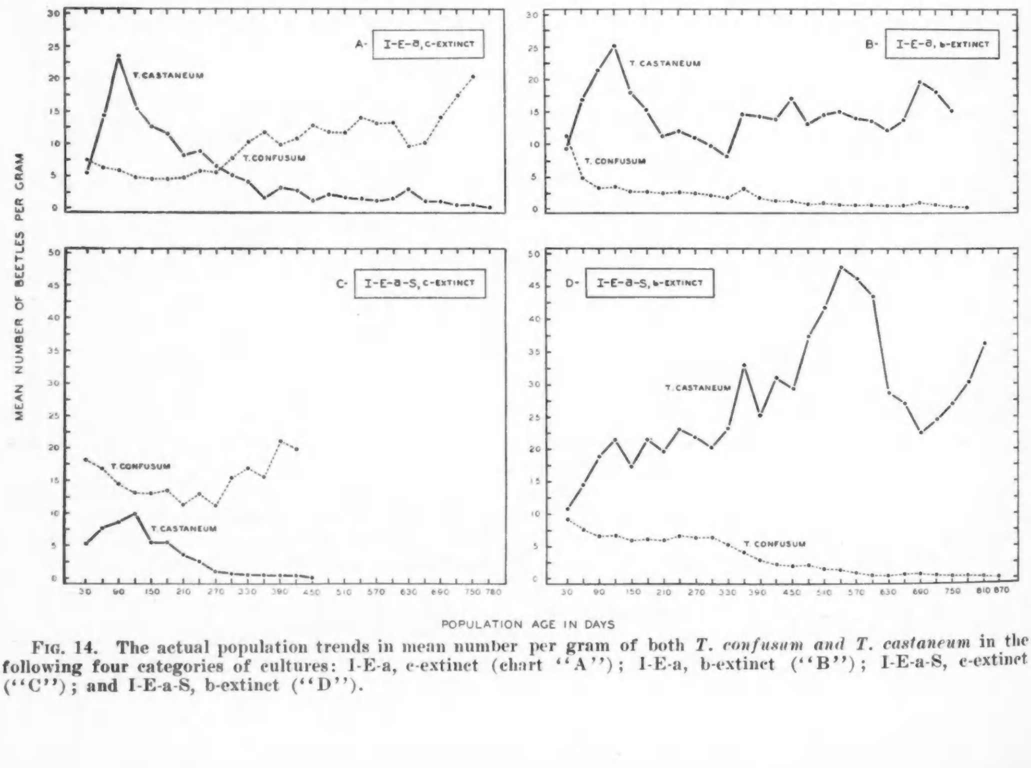

FIG. 14. The actual population trends in mean number per gram of both *T. confusum and T. castaneum* in the following four categories of cultures: I-E-a, c-extinct (chart "A"); I-E-a, b-extinct ("B"); I-E-a-S, c-extinct ("C"); and I-E-a-S, b-extinct ("D").

result in non-parasitized cultures. The pattern of events, having been sufficiently discussed for the former group, needs no further elaboration. The pattern for the latter group (sterile) is dissimilar to any thus far seen and requires brief description. These six, I-E-a-S populations behave very differently from their infected and sterile counterparts. The significant feature is that *T. confusum*, rather than *T. castaneum*, is the abundant form from the time of the first census, a dominance which is maintained until *T. castaneum* completely disappears. Furthermore, this disappearance occurs sooner than that seen for any other cultures of any experiment: the mean time is 320 days, the median, 315 days, and the range, 210-450 days. It seems evident that the factors operating to produce a result of this sort are different, in intensity and combination at least, from those already outlined.

With Adelina gone, *T. castaneum* normally would be expected to multiply abundantly as it does in I-C-c-S and, as it does after day-150, in I-E-a-S (b-extinct). Clearly, this does not happen, the reason for which is obscure. Is *T. castaneum* in these replicates inferior in some way even though it is not burdened with parasitization and does this "inferiority" then allow *T. confusum* to reproduce very effectively from the beginning on? Or, does removal of Adelina afford, in these instances, just enough of an added stimulus for *T. confusum* so that it goes ahead to out-compete its associate? The first alternative seems unlikely because it occurs too often to be mere happenstance and because no evidence of such "inferiority," apart from that induced by infection, has been unearthed. The second alternative has something to support it in that, as we have just seen, *T. castaneum* does show some gain during its early period of growth in the b-extinct, I-E-a-S group, and, it might be argued, this gain is sufficient to boost the species into its position of dominance. But this too is not a satisfying explanation for it does not identify causal factors nor does it indicate why the respective densities of the two species are reversed relative to each other after just thirty days of co-existence. This last point really states the crux of the problem and, if answered, would go a long way toward clarifying the whole matter.

About all that can be said at this time beyond merely describing the observed population trends, is to indicate (1) that *T. confusum* when uninfected drives out *T. castaneum* about one-third of the time and in the process builds up relatively large populations at an early date; (2) that this extinction pattern is of a different configuration than that seen for the parasitized populations which require a low density induced by Adelina at about day-300 before the species dies out; and (3) that, taken as a group, the extinctions occur sooner than those characteristic of the other experimental cultures.

(3) *I-E-a-S (b-extinct) compared with I-E-a-S (c-extinct).*—These two groups of sterile cultures, one involving the extinction of *T. confusum* in two-thirds of the cases and the other involving the extinction of *T. castaneum* in one-third of the cases, have been discussed sufficiently in the preceding sections so that only adumbration is required here. When the data for the two groups are graphed in terms of mean number per gram, the two following observations are worth noting:

(a) The density of *T. castaneum* in the b-extinct sample is always greater than in the c-extinct sample. For the former, this species starts its exceptional growth at day-300 and, without ever passing through a period of depression, soon attains the massive populations already described for the sterile controls. *T. confusum* starts out higher (by day-60) than it does in infected cultures, an interesting point stressed earlier, and maintains something of an equilibrium until the three-hundredth day, at which time it starts a decline that coincides exactly with the growth of its competitor. The curves for these two species (b-extinct group) suggest (1) that *T. confusum* is more abundant during the first year than it would be if Adelina were present; (2) that *T. castaneum* is not quite as abundant over the same interval as it would be if *T. confusum* did not display such a heightened density; and (3) that *T. castaneum*, unencumbered by the parasite, eventually achieves such large populations despite the presence of its competitor that the latter disappears from the cultures.

(b) The curious situation in the c-extinct, sterile sample was dealt with in the last section. In sum, this is characterized by the immediately large populations of *T. confusum*, the essential persistence and exaggeration of this condition, the early reduction in numbers of *T. castaneum*, and the relatively rapid dying-out of this species. The data show that *T. castaneum* does increase slightly between day-30 and day-120 and that during this interval *T. confusum* declines somewhat. This substantiates a general principle emerging from the mixed-species cultures, namely: that when one species trends upward, the other species trends downward, and *vice-versa.*

CONVERSION OF MIXED-SPECIES POPULATIONS INTO SINGLE-SPECIES CONTROLS

It is valuable to compare the total size of those cultures that had been experimental populations with the total size of counterpart controls of the same age. These comparisons are presented in Table 28 for all groups except series III. The last are omitted because there are only two replicates for each sample. The age selected for analysis was arbitrarily chosen to include the maximum number of cases for each group. The table lists the mean numbers of beetles per gram and, when N is large enough, their respective probable errors.

The findings are straightforward. There are no significant differences in terms of total size between the populations that had recently been in competition with another species of Tribolium (formerly, experimentals) and those that had never experienced such an association (controls). To state the point differently, such competition imposes no lasting effect upon the species that survives. The latter goes ahead

TABLE 28. Mean total number of beetles per gram from cultures originally of both species after these become single species population, compared with appropriate controls of the same age.

Populations:	Age at Comparison	Mean per Gram	Mean Difference Between Controls and Experimentals	n
I-E's (c extinct)	840	18.6± 0.6303	0.8± 0.95	30
I-C-b	840	19.4± 0.7193		19
I-E's (b extinct)	840	12.4	1.0	5
I-C-c	840	13.4± 0.7652		13
I-E-a-S (c extinct)	840	21.9		6
I-C-b-S	840	20.8± 0.6946	1.1	16
I-E-a-S (b extinct)	840	45.4± 4.41	1.8± 4.8	11
I-C-c-S	840	47.2± 2.13		16
II-E's (c extinct)	1140	15.3± 0.4458	1.6± 1.8	22
II-C-b	1140	16.9± 0.3877		17

to assume the normal pattern that typifies it under these conditions of husbandry.

DISCUSSION

The studies of single-species control cultures of *Tribolium confusum* and *Tribolium castaneum* grown apart under similar and essentially constant environmental conditions have shown that these two flour beetles maintained themselves successfully, eventually established equilibria characteristic for each, and exhibited no more variability, and perhaps less, than would be expected for ecological data of this sort. In addition, the sporozoan parasite, *Adelina tribolii*, was demonstrated to have a dramatic effect especially upon populations of *T. castaneum.* When Adelina had attained the requisite saturation within cultures of this beetle, the host dropped in numbers, and, after partial recovery and as if in adjustment to the parasite, then carried on at reduced density. Removal of the parasite also completely removed this low depression and permitted the beetle to attain an abundance considerably over twice that displayed by counterpart, but infected, populations. Adelina did not influence the behavior of *T. confusum* in anything like the same way. When parasitized, this beetle does not exhibit the depression mentioned above and, even when cultured under parasite-free conditions, does not produce larger total populations. It was shown for both Tribolium species that the relative abundance of imagoes, as indexed by percentages, increased something in the order of twenty per cent in complete absence of infection. Many other facts about the control populations were established earlier, but the above, sketched broadly as they are, are sufficient for present purposes.

When *T. confusum* and *T. castaneum* are placed together in competition, one of the two always becomes extinct. This may occur as early as 180 days after starting the experiment or, rarely, as late as 1470 days; but occur it does. Furthermore, it is not a particular species which invariably dies out as has been made abundantly clear. After extinction takes place, the population assumes "control behavior" by which is meant that it does not differ significantly from cultures of the same age and species that have never had the experience of competition in their past history.

The conclusion thus seems clearly established that competition between the two species always ensues when they are brought together as components of the same ecosystem. This is to be expected on the basis of their ecology. They inhabit the same medium to which both are well adapted individually; they exploit the same source of food; their life-histories are fundamentally quite similar; they are not divergent as to size, although *T. confusum* is somewhat larger; their patterns of reproduction, and so far as known, their mortality, are generally alike; and they are undoubtedly closely related in the taxonomic sense. With these facts in mind, it could be forecast *a priori* that stringent competitive pressures would arise between the two populations and that these would probably lead to definite end-results in respect of species survival (Crombie 1945, 1946, 1947). Such end-results have been classified and, in a large way, some of the factors, or factor-complexes at least, have been identified.

The story is complicated, although not rendered insolvable, by the finding that competition does not invariably result in only one outcome. This is not regarded as surprising—in fact, it might well be expected on the basis of general knowledge of population ecology as well as on the basis of the fact that *T. confusum* and *T. castaneum* considered individually as species are both successful groups with wide zoögeographic ranges (see Elton 1946, Lack 1937, Williams 1947).

The disclosure that either species may die in the presence of the other (although with different frequencies depending upon the experimental design) suggests that, to occur, the extinction process requires an antecedent, reticulum of related events which, for a specific type of population, typically unfold in a particular way but which, in exceptional cases, may be so altered as to produce the dying out of the other organism.

At least four categories of factors are operating within these mixed-species populations. These are:

(1) Competition exerted against *T. confusum* by *T. castaneum.*
(2) Competition exerted against *T. castaneum* by *T. confusum.*
(3) The presence or absence of Adelina in relation to *T. confusum.*
(4) The presence or absence of Adelina in relation to *T. castaneum.*

Obviously, these four factors interact as a nexus, their intensity and effectiveness varying with time as a density-dependent function (Nicholson 1933, Schwerdtfeger 1942, Smith 1935, Thompson 1939, Varley 1947). Further, it should be possible to dissect them experimentally. Competition means nothing in the analytical sense unless the operations comprising it are identified and quantitatively evaluated. Parasitization, if present, has maximum meaning

when the degree and pathogenicity of infection pressure is assayed relative to the differential susceptibilty of both species and to the age and history of the ecosystem considered in its entirety. As stressed several times in this report, answers to such matters cannot be presented here but depend on a program of further research, a segment of which is now in progress.

It is evident that the two species of flour beetles compete with each other and in this way alter their respective futures as populations. With the parasite present, and during the earlier stages of growth, *T. castaneum,* perhaps in part because of its higher reproductive capacity, increases, while *T. confusum* contracts. *T. castaneum* then suffers a considerable decline owing to the heightened mortality consequent upon the build-up of Adelina after which its associate gradually starts to multiply. The former species eventually attains a critically low density and is driven from the cultures when in this vulnerable state. If, as occasionally happens, the parasite does not bring about a minimum density sufficiently within the critical limits, *T. castaneum* stages a recovery of the sort characteristic of control cultures, and this leads to the extinction of *T. confusum.* Removal of Adelina reverses the frequency of occurrence of these events largely (1) by eliminating that depression in numbers exhibited by infected controls and experimentals at about the three-hundredth day, and (2) by enabling this species to establish populations of much larger size. The last phenomenon, of course, further increases the competition pressure exerted against *T. confusum.* However, as we have seen, *T. confusum* also appears to profit to some extent from the absence of the parasite and about a third of the time, is able to inhibit *T. castaneum* enough so that its early decline and extinctions is initiated. This particular sequence is not understood at the moment.

Before concluding this discussion, it is germane for purposes of orientation to speculate briefly about certain types of factors that may prove to be involved in the phenomenon of interspecies competition explored in this study. As general background, it should be remembered that both flour beetle populations are competing for space and for food in a limited environment in which, as single species, they maintain indefinitely an equilibrium so long as the medium is regularly renewed and the physical environment remains favorable.

Following are some possible ways that the two species of Tribolium could influence each other when grown together:

(1) They may exploit in differing degrees the quantity and/or nutritive quality of the available food supply. This could be brought about by interactions ("coactions") between the beetles and induce a change in their physiology, or, it could alter the milieu directly ("conditioning"). (Park 1941).[7]

(2) They may be differentially tolerant to simple crowding both inside the medium and on its surface. This could impose an effect upon their fecundity, fertility, rate and success of post-embryonic development, imaginal mortality, and age-distribution. (Park 1933, Boyce 1946).

(3) The presence of a competitor could modify the intraspecies relations in a way that these would diverge markedly from those characteristic of control cultures.

(4) There may exist actual behavior coactions between the two forms that inhibit one, inhibit both, or favor one and which undoubtedly would vary with the density and ecological age of the ecosystem. For example, such coactions could involve,

(a) alteration of the temperature, moisture content, and oxygen concentration *within* the medium ("microclimate") from that obtaining in the controlled incubators in such a way as to affect, differentially by species, the natality and/or mortality rates;

(b) differential predation in which, say, the larvae and imagoes of one species might consume the eggs and pupae of the other at a rate statistically higher than that directed against their own kind;

(c) differential interference with copulation or fecundation; and

(d) differential conditioning of the medium (Crombie 1945). This might concern the reduction of available food, the elaboration of environmental poisons, such as excrement and carbon dioxide, or comminution of the flour itself.

Much remains to be done before it can be said that interspecies competition in the genus Tribolium is well understood. But it is hoped that a start has been made and that future analytical research, wherever conducted, will contribute to this general problem which, in the author's opinion at least, is an important one for population ecology and evolution.

SUMMARY

(1) The census history of 211 laboratory populations of the flour beetles, *Tribolium confusum* and *Tribolium castaneum,* maintained in three volumes of favorable medium was accurately followed for a period of about four years with counts made every thirty days. Some of these populations consisted only of *T. confusum* ("controls"), others were exclusively *T. castaneum* ("controls"), and still others contained both species brought together in competition in a shared environment ("experimentals"). The medium was regularly renewed at each census and all cultures were kept in constant temperature incubators. In addition, certain control and experimental populations ("steriles") were rendered free of a sporozoan parasite, *Adelina tribolii,* that inhabits with consequent pathogenicity the haemocoels and other tissues of the beetles and is distributed as

[7] For *T. castaneum* at least, there is a suggestion that limitation of food supply does not play a significant rôle in controlling the equilibrium density achieved by these populations. The point was made explicit in the section on single-species populations and re-affirmed in the section on mixed-species populations. It will be remembered from the discussion of the sterile controls of *T. castaneum* (I-C-c-S) that the density increased nearly three times when parasitization was eliminated. This occurred without any alteration in the total amount or nutritive quality of the flour-yeast medium.

inactive, but infectious, oöcysts throughout the flour. Since this parasite is a potent source of mortality, especially for *T. castaneum*, it was necessary to evaluate the statistical effect of its presence and absence in the ecosystem before the findings could be interpreted.

(2) Single-species, control populations of *T. confusum* and *T. castaneum* grew successfully and eventually established equilibrium densities that were maintained for the duration of the study. *T. confusum* stabilized at a higher total density than did *T. castaneum*. The latter exhibited a marked depression in numbers at about the three-hundredth day from which it typically recovered. This depression is attributed to increased mortality resulting from parasitic infection. Evidence is advanced, for *T. confusum* particularly, that density is inversely proportional to the total volume of medium.

(3) The absence of the parasite (Adelina) influenced the populations of the two beetles in different ways. *T. castaneum*, when uninfected, attained equilibria nearly three times greater than those characteristic of counterpart, infected cultures. Along with this went a complete removal of the depression mentioned in the paragraph above. On the other hand, *T. confusum*, when uninfected, maintained populations that did not differ significantly in terms of total size from the parasitized controls. Sterile cultures of both species possessed about twenty per cent more imagoes than did infected controls.

(4) Data are presented for all single-species cultures that analyze the variability within and between census counts both in respect of the total period of observation and for selected census intervals.

(5) Data are presented that describe the percentage composition of immature relative to mature stages for the various cultures, and these are discussed with reference to the design of the program.

(6) For experimental cultures in which interspecies competition is established, it is shown that one species of beetle *always* becomes extinct under these conditions, after which the surviving form then assumes a census trend statistically identical with comparable controls. However, not always the same species dies when faced with the competitive pressures of its associate. Typically, but with exceptions which are carefully dealt with, *T. castaneum* becomes extinct when Adelina is present, and *T. confusum* becomes extinct when Adelina is absent.

(7) The phenomenon of interspecies competition in Tribolium is discussed and the known facts are ordered into a preliminary hypothesis intended to partially collate the observed results.

(8) Future areas of research, analytical in character, are broadly sketched.

LITERATURE CITED

Bhatia, M. L. 1937. On Adelina tribolii, a coccidian parasite of Tribolium ferrugineum F. Parasitology **29**: 239-246.

Boyce, Janet Mabry. 1946. The influence of fecundity and egg mortality on the population growth of Tribolium confusum Duval. Ecology **27**: 290-302.

Chapman, R. N. 1933. The causes of fluctuations of populations of insects. Proc. Haw. Ent. Soc. **8**: 279-297.

Chapman, R. N., & Lillian Baird. 1934. The biotic constants of Tribolium confusum Duval. J. Exp. Zool. **68**: 293-304.

Crombie, A. C. 1945. On competition between different species of graminivorous insects. Proc. Roy. Soc. (B) **132**: 362-395.

1946. Further experiments on insect competition. Ibid. **133**: 76-109.

1947. Interspecific competition. J. Anim. Ecol. **16**: 44-73.

Dick, John. 1937. Oviposition in certain coleoptera. Ann. Applied Biol. **24**: 762-796.

Elton, Charles. 1946. Competition and the structure of ecological communities. J. Anim. Ecol. **15**: 54-68.

Ford, John. 1937. Research on populations of Tribolium confusum and its bearing on ecological theory: a summary. J. Anim. Ecol. **6**: 1-14.

Good, N. E. 1936. The flour beetles of the genus Tribolium. U. S. Dept. Agr. Technical Bull. **498**: 1-57.

Hesse, E. 1911. Sur le genre Adelea à propos d'une nouvelle coccidie des oligochètes. Arch. Zool. Exp. Gén. **7**: xv-xx.

Holdaway, F. G. 1932. An experimental study of the growth of populations of the "flour beetle," Tribolium confusum Duval, as affected by atmospheric moisture. Ecol. Monogr. **2**: 261-304.

Kollros, Catharine Lutherman. 1944. A study of the gene, pearl, in populations of Tribolium castaneum Herbst. Doctorate dissertation: University of Chicago Libraries.

Lack, David. 1947. Darwin's finches. Cambridge: 1-208.

Nicholson, A. J. 1933. The balance of animal populations. J. Anim. Ecol. **2**: 132-178.

Park, Thomas. 1933. Studies in population physiology. II. Factors regulating initial growth of Tribolium confusum populations. J. Exp. Zool. **65**: 17-42.

Park, Thomas. 1934. Observations on the general biology of the flour beetle, Tribolium confusum Duval. Quart. Rev. Biol., **9**: 36-54.

1941. The laboratory population as a test of a comprehensive ecological system. Ibid., **16**: 274-293, 440-461.

Park, Thomas, & William Burrows. 1942. The reproduction of Tribolium confusum Duval in a semisynthetic wood-dust medium. Physiol. Zool. **15**: 476-484.

Park, Thomas, & Marion Biggs Davis. 1945. Further analysis of fecundity in the flour beetles, Tribolium confusum Duval and Tribolium castaneum Herbst. Ann. Ent. Soc. Amer. **38**: 237-244.

Park, Thomas, E. V. Gregg, & C. Z. Lutherman. 1941. Studies in population physiology. X. Inter-specific competition in populations of granary beetles. Physiol. Zool. **14**: 395-430.

Pearl, Raymond, Thomas Park, and J. R. Miner. 1941.

Experimental studies on the duration of life. XVI. Life tables for the flour beetle, Tribolium confusum Duval. Amer. Nat. **75**: 5-19.

Riley, W. A., & Laurence Krogh. 1922. A coelomic coccidian of Tribolium. Anat. Rec. **23**: 121. (abstract)

Schwerdtfeger, F. 1942. Über die Uraschen des massenwechsels der Insekten. Zeit. f. angewandte entomologie **28**: 254-303.

Smith, H. S. 1935. The rôle of biotic factors in the determination of population densities. J. Econ. Ent. **28**: 873-898.

Stanley, John. 1946. The environmental index, a new parameter, as applied to Tribolium. Ecology **27**: 303-314.

Thompson, W. R. 1939. Biological control and the theories of interactions of populations. Parasitology **31**: 299-388.

Varley, G. C. 1947. The natural control of population balance in the knapweed gall-fly (Urophora jaceana). J. Anim. Ecol. **16**: 139-187.

Wenyon, C. M. 1926. Protozoology. N. Y. 1-1563 (2 vols.)

White, G. F. 1923. On a neosporidian infection in flour beetles. Anat. Rec. **26**: 359. (abstract)

Williams, C. B. 1947. The generic relations of species in small ecological communities. J. Anim. Ecol. **16**: 11-18.

Yarwood, E. A. 1937. The life cycle of Adelina cryptocerci Sp. Nov., a coccidian parasite of the roach Cryptocercus punctulatus. Parasitology **29**: 370-390.